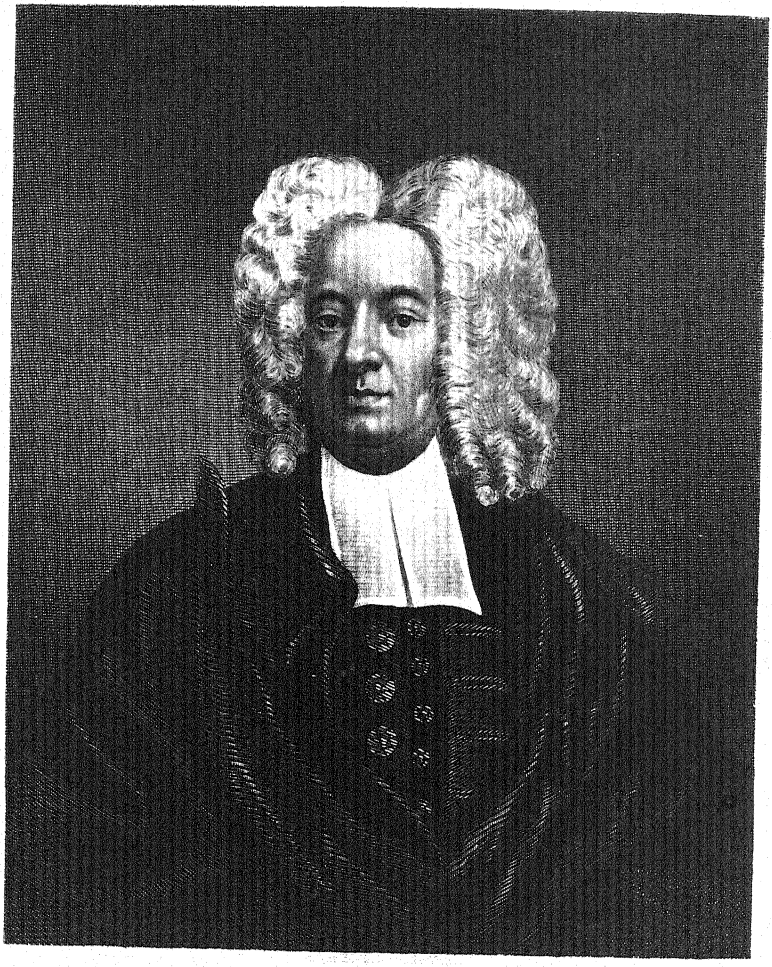
MORRIS ARBORETUM MONOGRAPHS

I

The Beginnings of Plant Hybridization



COTTON MATHER

THE BEGINNINGS OF PLANT HYBRIDIZATION

By

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FOREWORD

IN HER WILL providing for the establishment of the Morris Arboretum of the University of Pennsylvania, Miss Lydia Thompson Morris indicated among the purposes to be served by the Arboretum the increase of knowledge through research and the communication of knowledge through publication.

At present, the results flowing from investigations are in part finding an outlet in occasional volumes of Contributions from the Department of Botany and the Morris Arboretum of the University.

The more exhaustive investigations dealing with broader problems assume larger proportions and will be dealt with in volumes to be published from time to time in a series of Arboretum Monographs.

This book by Dr. Conway Zirkle of the Department of Botany and Geneticist to the Arboretum corrects serious errors in botanical history and greatly extends our knowledge of past thinking and doing in a very important line of plant investigation. It introduces the Monograph series.

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PREFACE

SEVERAL years ago my attention was called to a passage in Cotton Mather's essay, "On the Vegetables,"[1] which described two instances of plant hybridization, the spontaneous crossing of different color varieties of *Zea Mays* and the accidental contamination of squashes by the pollen of gourds. As this passage was obviously a very early record of plant hybridization which had not been mentioned by any historian of botany, I planned to reprint it in some genetical publication and thus incorporate it in our modern biological literature. In order to fit the quotation into its proper chronological place, I consulted Sachs's *History of Botany*, which is still our standard text, and found that Sachs apparently had known of but three contributions to plant hybridization before the time of Koelreuter (1761-1764). He had noted the crossing of two species of *Dianthus* by "a gardener in London" (Thomas Fairchild) and had cited the *Plantae Hybridae* of Haartman and the *Disquisitio de Sexu Plantarum* of Linnæus. On examining the original works referred to by Sachs, I was surprised to discover that he had misdated Fairchild's experiments, which he knew of only through a single reference in Bradley's *New Improvements of Planting and Gardening*. His treatment of Haartman's work was hardly adequate, and he misrepresented Linnæus completely. The other early hybridizers he had missed.

In fact the numerous contributions of the earlier plant breeders have never been collected or made available to modern geneticists. Even Roberts, who traced so clearly the development of pre-Mendelian genetics in his *Plant Hybridization before Mendel*, paid little attention to the hybridizers who preceded Koelreuter, although he did describe the work

[1] K. B. Murdock, Selections from *Cotton Mather*, New York, 1926.

of Richard Bradley in addition to those hybridization experiments mentioned by Sachs. Weatherwax (1923) noted the observations of Paul Dudley, and several modern authors have referred to Philip Miller's account of hybrid cabbages, but the other plant hybridizers who labored before the middle of the eighteenth century have been ignored. Today the fact is generally unknown that plant hybrids had been made and observed for forty-five years when Koelreuter undertook his classic experiments, and that many of these early observations had been reported with commendable care. Some few of these early investigators designed and executed their experiments as scientifically as did Koelreuter himself, and although many of them were extremely casual and did not bother to check their results or verify their speculations, a considerable knowledge of plant hybridization had accumulated by 1760.

In the following pages I have included all of the discussions of plant hybrids before 1761 which I have been able to find. Some of these contributions had existed only in manuscript and were published for the first time in a preliminary note in the *Journal of Heredity* (1934). The works are quoted in full, regardless of their merits, for most of them are in publications not available to the majority of geneticists. Some of these discussions of hybridity are intrinsically worthless, yet it is essential that we know of them if we are to understand the scientific standards of the early eighteenth century and appreciate the background of those investigators who gave us our first real knowledge of plant hybrids.

The history of science is developing rapidly into an independent discipline. Unfortunately, many of the elementary texts in the field have been oversimplified and thus rendered unnecessarily prosaic. It is well, of course, for us to evaluate the work of the past in terms of our present standards, and to emphasize the few outstanding contributions which, today, we accept as true; yet if we ignore the numerous minor con-

tributions, the often ludicrous errors of humorless investigators, we shall view the great discoveries of the past through a distorted perspective. Any picture we might make of our predecessors would be utterly false. For example, we can judge the early plant hybridizers more fairly if we remember that their zoölogical colleagues believed that eels hybridized with vipers, panthers with lions, horses with cows, and human beings with bears and apes.

I have received assistance in preparing this book from a great many sources, particularly in the many translations. For these I am indebted to Dr. George Strodach, Mrs. Elizabeth Harman Strodach, Dr. Hannah Croasdale, Miss Mildred Gilfillan, Miss Victoria Sposato, and my wife, Mrs. Helen Kingsbury Zirkle, who has also assisted in editing the manuscript and who has prepared the index. Professor Edgar Wherry has read the manuscript and suggested a number of valuable alterations. Many of the problems that arose during the compilation of the book were discussed with Professor Rodney Howard True and I owe much to his encouragement and support. I also wish to thank the *Journal of Heredity* for permission to reproduce material from two articles first printed in that magazine; and to acknowledge a University of Pennsylvania Faculty Research Grant, without which the work could never have been undertaken.

C. Z.

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I. PREHISTORIC HYBRIDS

THE word "hybrid" is probably derived from the Greek ὕβρις which means an insult or outrage, especially when the insult is offered to the Gods (*hubris*) or the outrage is connected with sex. Apparently the word acquired the meaning of "mongrel" through the general feeling that the production of such creatures was an outrage on nature. Even as late as the eighteenth century hybridization was not altogether reputable, and a number of the early plant breeders felt called upon to justify their attempts at crossing different species. There seems to have been a widespread belief that sexual intercourse between diverse types was an immoral perversion and that the production of new forms of life was an impious affront to the Deity, a tacit criticism of the original work of Creation. The origin of the word "hybrid" thus indicates that it was first used to designate mongrel animals, although at a very early date it was applied to human beings. The offspring of a Roman father and an Asiatic or African mother was a hybrid, as was the child born of union between a freeman and a slave. As an example of this usage the *Satires* of Horace may be cited where the term is applied to Persius, because of his mixed parentage. From 1:7;2:

"In what manner the hybrid Persius revenged the filth and venom of Rupsilius, surnamed King, is I think known to all the blind men and barbers." Later Pliny recorded the fact that Caius Antonius, a colleague of Cicero in the Consulship,

was nicknamed "hybrid"[1] because of his half-savage disposition.

The first species or variety crosses, due to a human agency, evidently occurred in the Neolithic Age. Indeed, cattle and dogs must have been hybridized almost as soon as they were domesticated. While our modern varieties of cattle are undoubtedly descended in great part from several sub-species of the urus or European wild ox (*Bos primigenius*), the earlest domestic cattle were of a very different breed. They were much smaller and resembled closely the eastern species, *Bos longifrons*. It is probable that cattle were first tamed in the East and brought into Europe during the neolithic migrations, the subsequent "grading-up" being secured by crossing domestic animals with the wild native stock (Watson, 1929). A number of modern breeds, however, such as the Shetland, Kerry, Jersey, and Brown Swiss still resemble the older neolithic cattle.

A few years ago it was generally held that the dog was a hybrid between the wolf (*Canus lupus*) and the jackal (*Canus aureus*), but a recent study of comparative tooth structure indicates that our domestic dogs are primarily descended from wolves (Miller, 1920). The dogs of all primitive peoples cross readily with the local wolves and soon grow to resemble them. The likeness of the Esquimau dog to the North American wolf and of the dog of the Hare Indians to the prairie wolf has been noted by Darwin (1868). The jackal, while not of equal ancestral importance, has undoubtedly contributed to some breeds of dogs. Thus the pariah dog of the East resembles closely the Asiatic jackal, and the dogs and the jackals of Africa have many anatomical features in common. The selective breeding of different types of dogs was well advanced by the beginnings of the early civilizations, for

[1] Suetonius (*Augustus* 19), Martial (*Epigrams* 6, 39, 20:8, 22) and Valerius Maximus (*Memorable Deeds, etc.* 8:6; 4) also apply the term "hybrid" to the progeny of human racial crosses.

Egyptian and Babylonian monuments depict several varieties of dogs which existed as early as 3000 B.C.

The first plant hybrids selected for crop betterment also appeared in neolithic times. The stone-age agriculturist had already cultivated the more useful of our domestic plants, and spontaneous hybridization probably furnished him with those valuable combinations of characters which distinguish our cultivated varieties from their wild ancestors. Hybridization could hardly have been deliberate in the absence of all knowledge of the function of pollen, and consequently the improvement of the cultivated plants must have been haphazard and dependent upon a series of lucky accidents.

One member of the Vegetable Kingdom, however, the stately date palm (*Phoenix dactylifera*), was conspiciously different from all other plants. To the Babylonians and Assyrians it was the Tree of Life, and to the medieval Arabs it seemed a connecting link between the animal and plant kingdoms. Today, it is the basic food plant of Mesopotamia, Arabia, and the oases of the Sahara. But the unique position of the date palm was due neither to its beauty nor its usefulness, but to the fact that it is dicœcious. In this plant the sexes are separated, and the female trees will not bear fruit if deprived of pollen from the male trees. In a state of nature, where palms are grown from seedlings, approximately 50 per cent of the trees are masculine, and enough pollen is produced to fertilize all the female trees. Wind pollination is very wasteful, however, for when the pollen is conserved and applied directly to the female flowers, one male palm will serve a hundred females. Thus the discovery of the efficacy of hand pollination enabled the date growers to increase the proportion of their fruit-bearing female trees from 50 per cent to 99 per cent.

Like many other fruit trees that have been under cultivation for a long time, the date palm is extremely heterogenous;

in fact, it is one of the most variable of all plants, and today there are over 5,000 named varieties (Popenoe, 1914). These commercially valuable dates do not breed true from seeds, and in this way they betray their hybrid character, although no internal evidence of hybridity is really needed, for the present methods of date culture assure a variety cross every time pollination is effected.

The different varieties of dates are classified by the characteristics of the fruit. As male trees bear no fruit they cannot be identified in this manner and, inasmuch as the female trees do not breed true, the different male varieties cannot be classified according to their descent. Both male and female varieties are propagated vegetatively, through suckers cut from the trunks of young trees. Thus males "beget" males and females "beget" females. As the two sexes are valued for very different qualities, they have been selected along somewhat divergent lines. Female strains are grown, of course, for the commercial importance of the fruit; the male trees simply as a source of pollen. Pollination is effected only because it is necessary for the maturing of the fruit, not because of any effect it may have upon the characteristics of the offspring. Walter T. Swingle (1904) has described some of the qualities which give the male varieties their relative importance in Egypt and North Africa. The following quotation is taken from the U. S. Department of Agriculture Bulletin No. 57:

> Some male trees produce more pollen than others, and are much preferable to use in pollinating. When once good sorts of males are found they should be propagated by offshots in the same manner as the female plants. In most parts of the Algerian Sahara no particular attention is paid to the propagation of suitable male palms, and in consequence pollen is scarce early in the flowering season and again later on, which often renders it necessary to procure pollen from neighboring orchards or even from other oases, sometimes at

considerable trouble and expense. In Tunis there is a male variety propagated by off-shoots called the Deglaoni used to pollinate late-blooming sorts. Another called the Bakar majahel was secured by Mr. D. G. Fairchild[2] in Egypt, and has been sent to the Co-operative Date Garden at Tempe, Arizona. It is said to be the only male palm which produced pollen at the right time to be used on all of the eight varieties of female dates grown about Ramley, Egypt.

The chief requisite of a male date palm is that it shall produce an abundance of pollen at the right time to be used in pollinating the female sorts that are grown. If date palms were propagated from seed, and still more if any attempt should be made to breed new and better sorts, it would be very desirable to secure male sorts capable of transmitting desirable characteristics to their offspring.

Variety crosses in the date palm were probably initiated shortly after the invention of artificial pollination. Just when this was first tried we do not know, although it must have been extremely early. It possibly antedated the invention of writing. Tylor (1890) was the first to call attention to the significance of those Assyrian bas-reliefs where winged deities are shown inserting the male spathe of the date into the female flower. Thompson (1924) has translated some of the records from the library of Ashurbanipal (667-622 B.C.) which show that pollination was then well understood. Bas-reliefs from the palace at Khorsabad (800-700 B.C.) illustrate clearly the actual pollination. Since we have learned the significance of these carved figures we can understand better

[2] David Fairchild (1903) has described the male varieties in Mesopotamia:

. . . A single male tree yields sufficient to fertilize the flowers of one hundred female trees, but there are especially productive male varieties whose pollen is more abundant, powerful, and has better keeping qualities than others. The names of three of these as given by Mr. Raphael Sayegh, of Basorah, to whom the writer is indebted for some valuable information, are: "Gunnami," "Wardi," and "Semaismi." Of these three, the first, "Gunnami," is considered the best, and is the only one which the old veteran date grower and buyer, Hadjii Abdulla Negem, of Abu Kassib, would recommend for planting. At Maskat, or the date valley of Semail, in the interior, a special variety of male is planted, but so far as could be learned it has no name except that of "Fachl," which means "male." In the region back of Guadur, called Key, the male variety in use is called "Gush." As young male plants of the best variety in each locality have been secured for introduction, it will be interesting to learn which sort will thrive best in America.

the descriptions of many of the ancient Semitic palaces and temples, where, literally, not one stone now rests upon another. We know that the Assyrian winged figures are cherubim, for Ezekiel has given us a detailed account of the anatomy of these celestial beings (Ezek. 1;8:10;8,21). Even Solomon's Temple at Jerusalem (1012-1007 B.C.) was decorated with alternate cherubim and palm trees (I Kings 6; 29,32,35: 7; 36: Ezek. 41; 37). It is not stated specifically in the description of this building that the cherubim were engaged in pollinating the flowers of the palms, but every remnant we have of this decorative motif shows them in this formalized pose.

Authentic records of pollination extend back to early Babylonian times. Pruessner (1920) has translated some business contracts of the Hammurabi period (2000 B.C.) which show that even then the male flowers of the date palm were an important article of commerce. The Code of Hammurabi itself mentions pollination. Scheil (1913) has translated an inventory of an orchard of palm trees dating from the fifth year of the reign of Gimil-Sin (2400 B.C.) which shows that at this still earlier time the males were grown apart from the females and that pollination had to be artificial. This inventory is the oldest document yet found which indicates that the sexuality of palms was recognized, although more ancient records show that dates had long been an important crop. Manishtusu (2800 B.C.) offered a special kind of date to his gods, and a Sumerian cylinder of the period of Queen Shubad (3500 B.C.) depicts the harvesting of dates (LeGrain 1929).

Other fruit trees also were hybridized by the ancients, and certain fruits were valuable only because they were hybrids. It is now thought that the banana was first cultivated for its edible stem (White 1930), but upon the spontaneous appearance of a seedless hybrid, the fruit acquired such a value that the original use of the plant was forgotten. The fig tree, too,

ASSYRIAN CHERUB IN ACT OF

was hybridized by means of the peculiar process of caprification which insured the fertilization of the valuable cultivated figs of the Smyrna varieties by the pollen of the wild fig (*Caprificus*), for without this pollen, the fruit falls from the trees before it is ripe. We do not know when this use of the wild fig was discovered. It is certainly much older than Herodotos (484-425 B.C.), for his very inaccurate description of fertilization in the date palm shows that he knew of caprification. From *Clio* (Bk. I):

> The palm is a very common plant in this country [Egypt] and generally not fruitful: this they cultivate like fig trees, and it produced them bread, wine, and honey. The process observed is this: they fasten the fruit of that which the Greeks term the male tree to one which produces the date. By this means the worm which is contained in the former enters the fruit, ripens and prevents it from dropping immediately. The male palm bear insects in their fruit, in the same manner as the wild fig tree.

2. THE FIRST MULES

A study of our domestic animals and plants reveals the fact that many of them have been modified by past hybridization. The actual records of variety and species crosses, however, are generally unreliable and even fantastic. Some few are sound, but these are frequently concealed in passages which have obviously been corrupted by copyists. The words themselves often have meanings far from obvious, and it is very necessary for us to get a picture of the writer's background before we can interpret his work. If we are to understand the slow growth of an accurate knowledge of hybridity, we must examine all of the records, those obviously fallacious as well as those we consider true.

The origin of fertile hybrids could easily be forgotten, particularly the origin of those which appeared before the dawn of history. The hybrid nature of the sterile mule, how-

ever, could not be overlooked, and we would expect that the earliest mention of mules would refer to known hybrids. In fact, the mule is the first animal whose hybrid origin was generally recognized, although an ambiguity exists, even in these records. We must have more than the word "mule" or "*mulus*" in an English or Latin translation before we can cite the original as an authentic record of a species cross. The poetical English renditions of the Classics are just inaccurate enough to make them useless as scientific records. As an illustration of this poetic license, we may quote some translations of what is perhaps the first passage which mentions mules. It is in the *Iliad* (Book I) in the passage which describes the Trojan allies. As translated by Chapman the passage reads:

> Pylaemen with the well-armed heart the Paphlagonians led
> From Enes, where the race of mules fit for the plow is bred.

Pope has it:

> The Paphlagonians Pylaemenes rules
> Where rich Henetia breeds her savage mules.

According to Blackie:

> Pylaemen, a shaggy-hearted Paphlagonian led
> His stout men from the Heniti, where sturdy mules are bred.

From these couplets we might infer that mules had the same disposition in 800 B.C. that they have today and that they were then used in farming. In fact, this passage is responsible for the statement that mules were first used in Mysia and Paphylagonia (*Encyc. Brit.* 18:959.1911). The more literal translation of Walter Leaf (1912), however, throws another light on the passage. Thus:

> The shaggy heart of Pyliamenes led the Paphlagonians from Eneti, whence comes the race of wild mules: these are they that owned Kytoros and inhabited Sesamon and dwelt in famed houses about the river Parthenois and Kromna and Aigialos and lofty Erythini.

Now the mule, which has been described as an animal with neither pride of ancestry nor hope of descendants, has more excuse for being wild than most animals; but he is the one animal which cannot exist in a state of nature. Obviously these wild mules were not sterile hybrids. Leaf points out that we translate as mule the Greek word ἡμίονος which literally means "half-ass" and that the wild species, *Equus onager*, might well appear to the Greeks to deserve this designation. Indeed, Aristotle (384-321 B.C.) knew of the two different animals called by the same name and clearly distinguished between the two in the *Historia Animalium*—From 6:36:1.

In Syria are found the so-called mules, a different race[3] from the hybrids between the horse and the ass, but resembling them in appearance and deserving the name from resemblance. Like the wild ass this wild mule is remarkable for its speed. The mules propagate among themselves, and a proof of this may be gathered from the fact that a certain number of them were brought into Phrygia in the time of Pharnaces,[4] the father of Pharnabazes, and the animal is still there. The number originally introduced was nine and there are three there at the present day.

Mules are mentioned several times in the *Odyssey*. They pulled the cart in which Nausicaa carried the family wash

[3] A curious account of the parturition of a mule is found in the third book of Herodotos. It is possible, of course, that this animal belonged to the species *Equus onager;* yet the very fact that the event was looked upon as a prodigy is evidence that she was a hybrid and that the incident was one of those rare occasions when a real mule breeds. From *Thalia* 151-153:

Darius being informed of this and having collected all of his forces, marched against them; and having advanced to Babylon, he besieged them, who were not at all solicitous about the event, for the Babylonians, mounting on the ramparts of the wall, danced and derided Darius and his army, and one of them spoke as follows, 'Why sit ye there, O Persians? Will ye not be off? For ye will take us when mules bring forth young.' One of the Babylonians said this, who never expected that a mule would breed. . . . (153.) Thereupon, in the twentieth month, . . . to Zopyrus, son of Megabyzus, the following prodigy happened: one of his sumpter mules brought forth young: but when the news was told him, Zopyrus himself, not believing it, went to see the foal, and having strictly charged his servants not to tell anyone what had happened, he considered on it.

Aristotle also described the wild mules in *de Mirabilis* 70:1, while Pliny (*Hist. Nat.* 8:69) quotes a description of them in Theophrastos.

[4] First half of fifth century B.C.

when she was inspired by Athena to rescue the shipwrecked Odysseus. In one passage in Book XXI, we can identify the mules with certainty as hybrids. This may be the first mention of real mules. It is taken from the account of how Odysseus obtained his famed bow.

In the long quest for these, Odysseus took the journey when he was but a youth. Iphitus, on the other hand, was seeking horses; for twelve mares had been lost, which had as foals twelve hardy mules. These afterwards became the death and doom of Iphitus when he met the stalwart son of Zeus, the hero Hercules, who well knew deeds of daring; for Hercules slew Iphitus in his own house, although his guest, and recklessly did not regard the anger of the gods nor yet the proffered table, but slew the man and kept at his own hall the strong-hoofed mares.

This account of the stolen mares and mules of Iphitus may constitute the oldest documentary evidence of hybridization in the Equideae, although mules are mentioned very frequently in the Hebrew Scriptures.[5] In the sixth century before Christ, however, the older Hebraic books were edited very thoroughly, which makes them, in their present form, younger than the *Odyssey*. If the original documents of Genesis are ever discovered, it is quite possible that the reference to the mules found by Anak in the wilderness (Gen. 36:24) will be older than any Homeric records of the hybrid.[6] It is somewhat surprising that mules should be mentioned so frequently in the Old Testament, for the Hebrews were expressly forbidden to experiment with hybridization. The mating of unlike types seems to have been considered a form of bestiality. From Leviticus 19:19:

Ye shall keep my statutes. Thou shalt not let thy cattle gender with a diverse kind; thou shalt not sow thy field with mingled seed;

[5] (Gen. 36:24, Ezek. 27:14, II Sam. 13:29, I Kings 1:33, 38, 44, 4:28, 10:25, 18:5, II Kings 5:17, Isa. 66:20, I Chron. 12:40, II Chron. 9:24, Zec. 14:15, Ezra 2:66, Neh. 7:68, Psalms 32:9, Esther 8:10, 14).

[6] St. Isidore of Seville quotes a tradition to the effect that mules were first made by Dana, a great-great-grandson of Esau. (See page 27).

neither shall a garment mingled of linen and woolen come upon thee.

Hesiod, who may have been contemporary with Homer, mentioned mules four times in his famous treatise on farming, the *Works and Days*. Hay must be gathered so that the oxen and mules may have fodder (line 605). The twelfth day of the month is auspicious for emasculating mules (line 787), the fourteenth for training them (791), while the twenty-ninth day is best for yoking both oxen and mules (815). These "half-asses" may have been the real hybrid mules, although the adjectives applied to them by Hesiod seem somewhat out of character. Hesiod's mules are "toil-enduring" and "patient," not "stubborn" or "misanthropic," so there is very real doubt as to what they actually were.

According to Aelianos, Empedocles (490-435 B.C.) recorded the mixing of unlike forms and, if true, this would certainly be one of the earliest records of hybridization. The passage which he quotes, however, need not be interpreted in this manner. It is possible that Empedocles was merely noting that the higher mammals seem to be built on similar plans. Under the heading "Bigeneribus" Aelianos writes,

Concerning double-descended and grafted or double-formed animals:

Empedocles, a naturalist writing of the peculiarities of animals, is the authority that certain creatures of double origin are born plainly uniting in one body compound characteristics. Indeed, these are the ones of which he chants:

"Many animals show a double descent in their limbs, in breast or head, or in some other part; just as is seen in the form of a bull before and after potency, or the reverse: in cattle are indeed traces of the human shape, and on the other hand in the human body there are traces of cattle."

An early record of true mules is found in Plato's *Apology* where Socrates is reported to have referred to the hybrid dur-

ing his trial (399 B.C.) in an attempt to refute the charge that he was an atheist:

But this is just the ingenious riddle of which I was speaking: the demigods or spirits are gods and you may say that I do not believe in gods, and then again that I do believe in gods: that is, if I believe in demigods. For if the demigods are the illegitimate sons of gods, whether by nymphs or by any other mothers, as is thought, that, as all men will allow, necessarily implies the existence of their parents. You might as well affirm the existence of mules and deny that of horses and asses. Such nonsense, Meletus, could only have been intended by you as a trial of me.

Aristotle also described the hybrid mules in a number of passages, and these formed the bases of most of the subsequent records. From the *Historia Animalium* (Bk. 6, Ch. 23):

When there is a cross between a horse and a she-ass or a jackass and a mare, there is much greater chance of a miscarriage than when the commerce is normal. The period for gestation in the case of a cross depends on the male, and is just what it would have been if the male had had commerce with a female of his own kind. In regard to size, looks and vigour, the foal is more apt to resemble the mother than the sire. If such hybrid connections be continued without intermittence, the female will soon go sterile; and for this reason trainers always allow of intervals between breeding times. A mare will not take the ass, nor a she-ass the horse, unless the ass or she-ass have been suckled by a mare; and for this reason trainers put foals of the she-ass under mares, which foals are technically spoken of as "mare-suckled." These asses thus reared, mount the mares in the open pastures, mastering them by force as stallions do.

A mule is fitted for commerce with the female after the first shedding of its teeth, and at the age of seven will impregnate effectually; and where connection has taken place with a mare, a "hinny" has been known to be produced. After the seventh year it has no further intercourse with the female. A female mule has been known to be impregnated, but without the impregnation being followed up

by parturition. In Syrophoenicia the she-mules submit to the mule and bear young, but the breed, though it resembles the ordinary one, is different and specific. The hinny or stunted mule is foaled by a mare when she has gone sick during gestation, and corresponds to the dwarf in the human species and to the after-pig or scut in swine; and as is the case with dwarfs, the sexual organ of the hinny is abnormally large.

From *De Generatione Animalium* (Bk. II, ch. 8):

. . . Again, when as a matter of fact, horse is born of horse, ass of ass, and mule of horse and ass in two ways according as the parents are stallion and she-ass or jackass and mare, why in the last case does there result something so "dense" that the offspring is sterile, whereas, the offspring of male and female horse, male and female ass, is not sterile? And yet the generative fluid of the male and female horse is soft. But both sexes of the horse cross with both sexes of the ass, and the offspring of both crosses are barren, according to Empedocles, because from both are produced something "dense" the "seeds" being "soft." If so, the offspring of stallion and mare ought also to be sterile. If one of them alone united with the ass, it might be said that the cause of the mule's being unable to generate was the unlikeness of that one to the generative fluid of the ass, but, as it is, whatever be the character of that generative fluid with which it unites in the ass, such it is also in the animal of its own kind. Then again, the argument is intended to apply to both male and female mules alike, but the male does generate at seven years of age, it is said; it is the female alone that is entirely sterile, and even she is so only because she does not complete the development of the embryo, for a female mule has been known to conceive.

Varro (118-30 B.C.) also thought that the mule occasionally bred, and again the hybrid mule was confused with the "wild mule." From *De re rustica:*

So strike off, if you like, in the case of mules, the two things, impregnation and foaling. "Foaling?" said Vaccius, "as though one didn't sometimes hear of a mule having foaled at Rome!" I, to support him, put in the statement of Mago and Dionysios to the effect that mules

and mares are delivered in the twelfth month after they have conceived. "And so," said I, "if parturition of a mule be with us in Italy a portent, all countries do not agree with us in thinking it one. Swallows, moreover, and storks, which breed in Italy, do not so in all countries. You know, of course, that the Syrian date palm, which bears in Judæa, cannot do so in Italy." "But," said Scrofa, "if you prefer to make up the number eighty-one without reference to the parturition of mules and the rearing of their young, there is a way of filling up the two gaps, . . ."

"There is little to be said about them," answered Murrius, "for both mules and hinnies are mongrel-grafts not springing from roots of their own kind. For from mare and he-ass comes a mule, while from horse and she-ass a hinny."

Columella (30-40 A.D.) in his version of *De re rustica* also described the breeding of foreign mules, but there is little doubt that he was himself familiar with the hybrid. Thus:

But some authors not to be concealed, as *Marcus Varro*, and, before him, *Dionysius* and *Mago*, have related that, in some countries in *Africa*, the breeding of mules is as far from being looked upon as prodigies by the inhabitants as that of mares is with us.

Pliny also described mules, and they were mentioned by almost every medieval writer on Natural History.

3. FANTASTIC ANIMAL COMBINATIONS

Many other species crosses were described by classical writers—both real crosses and fabulous mixtures of distantly related forms. The facility with which dogs and wolves interbred was generally noted, and the mention of this cross in the Zend-Avesta (700-400 B.C.) is certainly one of the earliest of all records of hybridization. From the Vendidad: *Fargard XIII = (The Dog) — VII.*

41. O Maker of the material world, thou Holy One! Which of the two wolves deserves more to be killed, the one that a he-dog begets of a she-wolf, or the one that a he-wolf begets of a she-dog?

Ahura Mazda answered: "Of these two wolves, the one that a he-dog begets of a she-wolf deserves more to be killed than the one that a he-wolf begets on a she-dog.

42. "For the dogs born therefrom fall on the shepherd's dog, on the house-dog, on the *Vohunazza* dog, on the trained dog, and destroy the folds; such dogs are more murderous, more mischievous, more destructive to the folds than any other dogs.

43. "And the wolves born therefrom fall on the shepherd's dog, on the house-dog, on the *Vohunazza* dog, on the trained dog, and destroy the folds; such wolves are more murderous, more mischievous, more destructive to the folds than any other wolves."

If Aristotle's writings on animal hybridization had ended with his description of the mule, his contribution would have stood on a much higher scientific plane. As matters stand, we must rate his credulity with Pliny's. Yet he gives us a very accurate picture of the general beliefs of the fourth century before Christ. In describing Libya he writes (*Hist. Animal.*, Bk. 8, Ch. 28):

It would appear that in that country animals of diverse species meet, on account of the rainless climate, at the watering-places, and there pair together; and that such pairs will often breed if they be nearly of the same size and have periods of gestation of the same length. For it is said that they are tamed down in their behaviour towards each other by extremity of thirst. And, by the way, unlike animals elsewhere, they require to drink more in winter-time than in summer: for they acquire the habit of not drinking in the summer, owing to the circumstance that there is usually not water then; and the mice, if they drink, die. Elsewhere also bastard-animals are born to heterogenous pairs; thus in Cyrene the wolf and the bitch will couple and breed; and the Laconian hound is a cross between the tiger and the bitch, not the first cross, but a cross in the third generation; for they say that the first cross is a savage creature. They take the bitch to a lonely spot and tie her up: if the tiger be in an amorous mood he will pair with her; if not, he will eat her up, and this casualty is of frequent occurrence."

The story of the queer matings which took place at the North African water-holes was repeated for nearly two thousand years. Buttressed by Aristotle's enormous authority it stood well beyond the reach of skepticism. In the following passage from *De Generatione Animalium*, Aristotle shows that his conception of sexual reproduction was in no way in advance of his times. He believed that the function of the female was mainly nutritive, and that her relationship to the foetus was the same as that of the ground to the growing crops. His failure to interpret correctly the pollination of the date palm is thus due not so much to his ignorance of sex in plants as to his misunderstanding of sexual reproduction in general. (Book II, Chapter 4)—

. . . For this reason if animals of different kind are crossed (and this is possible when the periods of gestation are equal and conception takes place at nearly the same season and there is no great difference in the size of the animals), the first cross has a common resemblance to both parents, as the hybrid between fox and dog, partridge and domestic fowl, but as time goes on and one generation springs from another, the final result resembles the female in form, just as foreign seeds produce plants varying in accordance with the country in which they are sown. For it is the soil that gives the seeds the material and the body of the plant.

(Book II, Chapter 7.)

Natural intercourse takes place between animals of the same kind. However, those also unite whose nature is near akin and whose form is not very different, if their size is much the same and if the periods of gestation are equal. In other animals such cases are rare, but they occur with dogs and foxes and wolves; the Indian dogs also spring from the union of a dog with some wild dog-like animal. A similar thing has been seen to take place in those birds that are amative, as partridges and hens. Among birds of prey hawks of different form are thought to unite, and the same applies to some other birds. Nothing worth mentioning has been observed in the inhabitants of the sea, but

the so-called "rhinobates" especially is thought to spring from the union of the "rhine" and "batus." And the proverb about Libya, that "Libya is always producing something new," is said to have originated from animals of different species uniting with one another in that country, for it is said that because of the want of water all must meet at the few places where springs are to be found, and that even different kinds unite in consequence.

Of animals that arise from such union all except mules are found to copulate again with each other and to be able to produce young of both sexes, but mules alone are sterile, for they do not generate by union with one another or with other animals.

Hybridization in pigeons was known to occur in classical times, and Varro describes the variety crossing which was a regular practice among Roman farmers. From *De re rustica:*

. . . Hence the wild variety mostly haunt turrets, flying up to them from the fields and back again as the fancy takes them. The other kind of pigeon is less shy, for it feeds contentedly at home about the doorstep. This is generally white, while the other, the wild kind, is of different colours, but not white. From the union of these two stocks comes a third, mongrel kind which is bred for profit.

Varro is free from most of the extravagances of Aristotle and Pliny. Another Roman writer, Lucretius (98-55 B.C.), shows a skepticism which is refreshing even if he carried it to the extreme of denying the possibility of hybridization. The hybrid monsters, whose existence he doubted, were generally believed in by his contemporaries. Lucretius based his doubts upon the great divergence of the parent types. A few lines after his beautifully lucid account of natural selection he wrote (translated by W. L. Leonard)—

> But Centaurs[7] ne'er have been, nor can be
> Creatures of twofold stocks and double frame,

[7] This skepticism of Lucretius was largely wasted. About 200 A.D., Aelian wrote his *De Natura Animalium,* describing the onocentaur in Bk. XVII, ch. 9, as follows:

Indeed it is now in my mind to describe the onocentaur relating the things I have learned through hearsay and fable; this onocentaur undoubtedly has a face similar to

Compact of members alien in kind,
Yet found with equal function, equal force
In every bodily part—a fact thou mayst,
However dull thy wits, well learn from this:
The horse, when his three years have rolled away,
Flowers in his prime of vigour; but the boy
Not so, for oft even when he gropes in sleep
After the milky nipples of the breasts,
An infant still. And later, when at last
The lusty powers of horses and stout limbs,
Now weak through lapsing life, do fail with age,
Lo, only then doth youth with flowering years
Begin for boys, and clothe their ruddy cheeks
With the soft down. So never deem, percase,
That from a man and from the seed of horse
The beast of draft, can Centaurs be composed,
Or e'er exist alive, nor Scyllas be—
The half-fish bodies girdled with mad dogs—
Nor others of this sort, in whom we mark
Members discordant each with each; for ne'er
At one same time they reach their flower of age
Or gain and lose full vigour of their frame,
And never burn with one same lust of love,
And never in their habits they agree,
Nor find the same food equally delightsome—
Sooth, as one oft may see the bearded goats
Batten upon the hemlock which to man
Is violent poison. Once again, since flame

man but surrounded by long hair; its neck and chest also have a human appearance; it also has on its chest distended breasts; it has shoulders, arms, elbows and hands and a chest and even loins like a human figure; its back, stomach, sides and hind legs are similar to those of an ass, and are ash colored as an ass, but the lower part of the stomach (over toward the side) is of a lighter shade: its hands perform a double duty, for when there is need for speed, they run ahead of the hind feet and consequently it cannot be overtaken by other four-footed animals; moreover, when it finds it necessary to seize food or to raise, place, seize or bind anything, the hands, which formerly were feet, are brought forth and then it does not walk but it sits. It is an animal of a serious, sad spirit; for, if it is captured, not enduring confinement, it refuses all food because of its desire for liberty, and it starves to death. Crates of Mysian Pergamon testifies that Pythagorus tells these things concerning the onocentaur.

Is wont to scorch and burn the tawny bulks
Of the great lions as much as other kinds
Or flesh and blood existing in the lands,
How could it be that she, Chimæra lone,
With triple body—fore, a lion she;
And aft a dragon; and betwixt, a goat—
Might at the mouth from out the body belch
Infinite flame? . . .

For though in earth were many seeds of things
In the old time when this telluric world
First poured the breeds of animals abroad,
Still that is nothing of a sign that then
Such hybrid creatures could have been begot
And limbs of all beasts heterogeneous
Have been together knit; because, indeed,
The divers kinds of grasses and the grains
And the delightsome trees—which even now
Spring up abounding from within the earth—
Can still ne'er be begotten with their stems
Begrafted into one; but each sole thing
Proceeds according to its own proper wont
And all shall consume their own distinctions based
In nature's fixed decree.

Lucretius' skeptical attitude in regard to hybridization was not mere supererogation. It was needed and needed badly. Two examples may be cited to illustrate the extreme credulity of the ancient Pagans and Christians. The first shows how a fantastic account of an impossible mongrel arose from a mere language difficulty. When the Book of Job was translated from Hebrew to Greek a mistake was made in rendering the eleventh verse of the fourth chapter. It happened that the Syriac word for lion resembled the Greek word for ant, and "The old lion perishes for lack of prey" became "The ant-lion perishes for lack of food," and thus a hybrid monster

was born in sacred literature. The existence of this creature was explained by the Physiologus, an early Christian treatise on natural theology dating from the last half of the second century. From section 20:

> The Physiologus relates about the ant-lion: his father hath the shape of the lion, his mother that of the ant; the father liveth upon flesh, and the mother upon herbs. And these bring forth the ant-lion, a compound of both, and in part like to either, for his fore part is that of a lion, and his hind part like that of an ant. Being thus composed, he is neither able to eat flesh like his father, nor herbs like his mother; therefore, he perisheth from inanition.

The second example of ancient credulity probably came from a misunderstanding of a passage in Aristotle. The passage (*Hist. An.* V, 4, 540 b) reads as follows: "Long animals devoid of feet, like serpents and eels, intertwine in coition, belly to belly." This was taken to mean that serpents and eels cohabited.

Pliny (Bk. IX, Ch. 23) shows the next stage in the legend. Thus, speaking of lampreys, he says—"If they chance to slip out of the water to drei land, the common sort is of opinion, that they engender with serpents." Nicander of Colophon (135 A.D.) refers to this cohabiting of serpents with eels, and Oppian (last half of second century) shows the myth well developed. From Oppian's *Halieutica:*

> Touching the Muraena (eels) there is a not obscure report that a Serpent mates with her, and that the Muraena herself comes forth from the sea willingly, eager mate to eager mate. The bitter Serpent, whetted by the fiery passion within him, is frenzied for mating and drags himself nigh the shore; and anon he espies a hollow rock and there vomits forth his baleful venom, the fierce bile of his teeth, a deadly store, that he may be mild and serene to meet his bride. Standing on the shore he utters a hissing note, his mating call; and the dusky Muraena quickly hears his cry and speeds swifter than an arrow. She stretches her eager from the sea, he from the land treads the gray

surf, and, eager to mate with one another, the two embrace, and the panting bride receives with open mouth the Serpent's head.

Athenaos of Naucratis in his famous *Deipnosophistae* (Bk. VIII, Ch. 12) also discusses the subject. Thus:

Andreas, in his treatise *On Poisonous Animals* says that only those lamphreys have a fatal bite which come from a viper, and they are less round and speckled. Nicander, in *Theriaca:*

"But there is the terror of the lampreys since it often bites the wretched fisher-folk and sends them in headlong flight from their skiffs to the sea when it suddenly darts up from the hold; if, to be sure, it is true that the lamprey leaves her pasturage in the sea and consorts with venomous vipers on the land." But Andreas, in his work *On Popular Superstitions,* says that it is not true that the lamprey moves into the lagoons and there mingles with the viper; for vipers do not feed in a lagoon, preferring sandy deserts. Nevertheless, Socrates in his work *On Animals* (it is in two books) agrees as to this mingling.

Claudios Aelianos described this same cross in *De Natura Animalium* which was written in the first half of the third century A.D.:

Concerning the Eel and the Viper

When the eel is full of passionate lust she goes on to dry land, and moved with a desire for a dangerous marriage, enters the hiding place of the male viper; and there they bind themselves together and are entwined in sexual union. Also the male viper, they say, goes down to the sea when aroused by the stimulus of lust; and as the youthful reveller makes a disturbance at the gate of his beloved with a flute, so the male viper calls his loved one with a hiss, and she comes from the sea, nature urging together inhabitants of different elements in one and the same desire for marriage.

The story is further developed:

Concerning the Viper and the Eel Which were Omitted Previously

How the male viper and the eel unite, the one coming from the

sea, the other crawling out from some hiding place, I remember I explained above; now there is more to say. When it is time for the viper to join with the eel in sexual embrace, he ejects and expels the poison by vomiting, so that the bridegroom is seen to be agreeable and charming; after that he calls the bride by giving a hiss, just as if to announce the nuptials with a kind of wedding song; and when they satisfy their mutual lust she indeed returns to the sea; he truly, sucking up and collecting his venom again, returns to his home.

Sometime during the fourth century Horapollo Nilous repeated the story in his false interpretation of the Egyptian hieroglyphics:

CXI. How a man that has commerce with persons of another tribe.

When they would symbolize *a man that has commerce with persons of another tribe*, they depict the LAMPREY, because it ascends out of the sea, and has commerce with the viper, and straightway returns to the sea.

The story of the eels and vipers got into Patristic literature. St. Basil, the Great (330-379 A.D.) used it to point a moral and to teach forbearance in holy matrimony:

. . . However hard, however fierce a husband may be, the wife ought to bear with him, and not wish to find any pretext for breaking the union. He strikes you, but he is your husband. He is a drunkard, but he is united to you by nature. He is brutal and cross, but he is henceforth one of your members, and the most precious of all.

Let husbands listen as well: here is a lesson for them. The viper vomits forth its venom in respect for marriage; and you, will you not put aside the barbarity and the inhumanity of your soul, out of respect for your union? Perhaps the example of the viper contains another meaning. The union of the viper and the lamprey is an adulterous violation of nature. You, who are plotting against other men's wedlock, learn what creeping creature you are like.

It might be interesting in this connection to note that St. Basil, in his same work, the *Hexameron*, denied that hybridization occurred among the fishes. Thus:

With them the reproduction of each species is invariable, and natures are not mixed. There are none of those unions which, on earth, produce mules and certain birds contrary to the nature of their species.

Achilles Tatios (c. 450 A.D.) seemed to be interested only in the romantic aspects of the story. From *The Loves of Clitopho and Leucippe*, Bk. I—

. . . A yet stranger mystery of Love is seen in reptiles, not merely in those of like race, but of different kind. The viper conceives a violent passion for a lamprey, which though in form a serpent, is to all intents and purposes a fish. When these reptiles wish to copulate, the viper goes down to the shore and hisses in the direction of the sea, which is a signal to the lamprey: she understands the sound, and issues from the water, but does not immediately hasten to her lover, knowing that he carries deadly poison in his teeth, but gliding up a rock, there waits until he has cleansed his mouth. After looking at one another for a space, the loving viper vomits forth the poison so dreaded by his mistress, and she upon perceiving this, descends and entwines him in her embrace, no longer dreading his amorous bite.

As time passed, the story of the philandering of the viper with the eel acquired such authoritative sponsorship, that no really learned person could doubt it. Each new account of the wonders of nature included it. The following quotation is taken from *De Animalium Proprietate* of Manuel Philes, a Byzantine naturalist of the fourteenth century:

Concerning Vipers

The male viper, wrapped up with its mate, after he accomplishes the most agreeable nuptials, lies dead prevented from a cruel slaughter of his spouse. For the wife keeping her anger secret seizes his head during the embraces in a bite of reciprocal venom. And by his death she may be pregnant. But, when somewhat later the young foetuses obstructed in emerging break from the maternal organs, is it somehow to avenge vigorously the death of the father?

The eel and the viper flaming with mutual love, the one coming

forth from his hiding places to the female, the other leaving the river bed. But before they unite with mutual joy the bridegroom gets rid of his venom by vomiting and with the sound of his hiss calls to the desired reward of conjugal bliss. Both replete after their pleasure, the viper sucks up the virus which he spit out and withdraws thereupon to the caverns of the earth and the eel swims through the wet streams.

Andrea Alciati (1492-1550), the great authority on jurisprudence, published his famous *Emblemata* in 1522, and this book passed through nearly forty editions during the next two centuries. The affair of the viper and the eel served as Emblem number 192. Even the viper parted with his venom in respect for marriage. From page 817-818 (Ed. published in Padua, 1661):

When the viper is in love it takes its stand upon the seashore and from its stomach vomits its deadly poison. The eel, aroused, acknowledges his great hissing and simultaneously desires the loving embraces of her mate. Greatest reverence must be rendered to wedlock: each mate owes the other indulgences in turn.

Fantastic as are these instances of hybridization, they give a true picture of the credulity of the ancient and medieval writers. Nature was rarely observed directly, and a belief tended to last indefinitely once it had achieved the dignity of the written word. For centuries the best-known scholars were those who copied the works of their predecessors, and assembled uncritically the errors along with some real knowledge. Pliny was one of the earliest as well as the most famous of these cyclopedists. His descriptions of hybrids are interesting not only in themselves, but also in the fact that they were copied literally for well over fifteen hundred years. His *History of the World* constituted the most popular treatise on Natural History in medieval Europe, and his use of the word "hybrid" to designate the product of a cross between wild and domestic swine resulted in the term being restricted

practically to this particular mongrel. From the *Historie of the World* (tr. by Holland, Pt. I, Bk. 8, Chap. 53):

There is no creature engendreth so soone with wild of his kind, as doth the swine: and in good sooth such hogges in old times they called Hybrides, as a man would say, halfe wild: insomuch as this tearme by a translation hath been attributed to mankind. For so was *C. Antonius*, colleague with *Cicero* in the Consulship, nicknamed and not in swine onely, but also in all other living creatures, looke where they be any tame and domesticall, you may find also wild and savage of the same kind; seeing that even of wild men there be so many sorts in divers places, as we have before said.

The next passage, obviously derived from Aristotle, confirms the reputation of Africa but defames the good name of the lioness. (Pt. I, Bk. 8, Chap. 16)—

The Lions are then in their kind most strong and courageous, when the hair of their main or coller is so long, that it covereth both necke and shoulders. And this cometh to them at a certain age, namely to those that are engendered by Lions indeed. For such as have Pards for their sires, never have this ornament, no more than the Lionesse. These Lionesses are very letcherous, and this is the very cause that the Lions are so fell and cruell. This, Affricke knoweth best, and seeth most; and especially in a time of great drought, when for want of water, a number of wild beasts resort by troopes to those few rivers that be there, and meet to-gether. And hereupon it is, that so many strange shaped beasts, of mixt and mungrell kind are there bred, whiles the males either perforce, or for pleasure, leape and cover the females of all sorts. From hence it is also, that the Greeks have this common proverbe, *That Affricke evermore bringeth forth some new and strange thing or other*. The Lion knoweth by sent and smell of the Pard, when the Lionesse his mate had plaid false, and suffered herselfe to be covered by him; and presently with all his might and maine runneth upon her for to chastise and punish her. And therefore when the Lionesse hath done a fault that way, shee either goeth to a river, and washeth away the strong and rank savour of the Pard, or else keepeth alloofe, and followeth the Lion farre off, that he may not catch the said smell.

From Bk. VIII, Ch. 49:

There is in Spain, but especially in the Isle of Corsica, a kind of Musmones, not altogether unlike to sheep having a shag more like the hair of goats, than a fleece with sheepes wooll. That kind which is gendered between them and sheep, they called in old time Umbri.

In the next century, Galen (130-200 A.D.) insisted that the hybrid progeny was intermediate between the two parental species. From *De Semine* (Bk. II, Ch. 1.)—

Now Athenaeus himself admits that, in the crossings of animals of different species, the offspring resemble the mother, not merely in a modification of their color, size, build, voice or other qualities of this sort; for these are superficial variations normal for an animal species. The whole appearance of those born from a mother (of a different species) is altered. If indeed a mare bears the offspring of an ass, the progeny not only resembles the father, but it also appears to be a blending of something from both parents. But if a fox bears the seed of a dog, that which is born is not a dog, but a blending of something from both species. And, what is much more important, is that which Athenaos confesses in his seventh book written on the progeny of animals, although I do not know how he perceived it. For he says that the offspring resemble the mother much more than the father, i.e., a he-mule born from a mare and a she-mule born from a jenny; when a fox is joined to a dog, if it is a male dog, that which is born has the appearance of a fox, but if the opposite it resembles the dog; so that whatever is born of a fox becomes a fox with the form of a dog and that which is born of a dog becomes a dog with the form of a fox. For if a he-goat breeds with a ewe he says that a ewe covered with rough hair is born as if the mother contributes not less to the offspring than the father, but even more. It is only necessary, however, for there to be present in the offspring not less from the mother [than from the father]. For the appearance does not change at all according to the species of an animal or a plant, but all such things are born according to the seeds.

During the twelve hundred years following Pliny, Europe made little progress. The classical authors were still respected

authorities, and during this time authority commanded real respect. About midway in this period, sometime between the years 622 and 633 A.D., St. Isidore of Seville wrote the *Etymologiarum sive Originum libri XX*. In an interesting passage in Book XII, he discussed hybridization, and cited a Jewish tradition to the effect that Dana first crossed the horse with the ass. If true, this would place the advent of the mule in the sixteenth or seventeenth century before Christ. From Bk. XII, Ch. I,—

. . . There are three kinds of horses, first, those suitable for fighting and working, second a vulgar type of the common herd suitable for hauling and not for being ridden, and a third type, a mule, sprung from the mixing of different races, and called hybrid because it is born of different beings. For in Greek it is that which guides in a circle the team grinding the heavy meal of the baker's kneading. The Jews assert that Dana, great-great-grandchild of Esau, was the first one to make herds of mares copulate with asses so that from this union mules, new animals contrary to nature, were born. Wild asses are also admitted to domestic asses for this purpose, and from the same kind of copulation are obtained very swift asses. Truly human diligence drives different animals together in coition, and thus by adulterous mating another race is obtained; and just so Jacob procured likenesses of colors contrary to nature. But on the other hand ewes conceive offspring resembling the images of their rams which they contemplate from above in the mirror of the waters. And, finally, this very thing is done in herds of horses, for those of noble birth are brought before the sight of those conceiving, by means of which they are able to conceive and create offspring resembling the noble stock. And in a like manner lovers of doves place those doves which are thought to be the most beautiful in the places where others dwell which generate forms of like beauty by seizing the vision. Hence it is that certain people command their pregnant women not to look upon shameful countenances of animals such as cynocephalos [a dog-headed ape] and monkeys lest they should bear offspring like those they met in their vision. This is the nature of females that whatever they look at they take up without thought in the extreme ardor of passion and

bring forth offspring of that kind. And indeed an animal in the practice of love transmits forms inward from without, and, saturated with them, it carries off a semblance of them in its own nature. Those animals are called hybrids which are born of diverse parents, as a mule from a mare and a he-ass; a burdo from a horse and a she-ass; hybrids from wild boars and pigs; tityrus from a ewe and a he-goat; mismo (muflone) from a female goat and a ram.

The quotation from St. Isidore illustrates very well the crude biological theories of the Latin Christians during the seventh century. The intellectual centers of Europe were declining during this period, but in the Mohammedan countries they were beginning to develop phenomenally. Yet the learning of the Arabs, although it soon became superior to that of the barbaric Latins and decadent Byzantines, seems trivial and superficial when judged by modern standards. Although the Arabic Natural History was superior to the European, it was highly speculative and romantic, and, as we might expect, the incidental discussions of hybrid animals had no intrinsic value. Today we are interested in these records because they illustrate the scientific standards of the times. A single example will be quoted here, a passage from the tenth-century work of Al-Mas'ūdī.

Al-Mas'ūdī (born before 912, died c. 957) was a traveler and geographer. He wrote *Meadows of Gold and Mines of Precious Stones* about the year 947, and in this book (ch. 33) he described the hybrid origin of the giraffe. Obviously the giraffe was not the type of animal that any serious-minded Diety would create, and the naturalists felt called upon to explain how such a creature could come into existence. (From Vol. III, pp. 3-5, ed. of 1864):

. . . The most common animal in these countries is the giraffe; but it generally lives in Nubia and is not found in any part of Abyssinia. There is no agreement as to the origin of the giraffe: some consider it a variety of camel; others say its build is the result of the union of

a camel and a panther; still others say it is a special and distinct race like the horse, the ass, and the ox, and is not the result of a cross, as is the mule which is formed by the mating of a horse with an ass. The giraffe is called in Persian *uchturgay*. One was sent from Nubia to the kings of Persia, just as later one was offered to the Arabian kings, to the first Abbasside Khalifs and to the governors of Egypt. This animal has very long front legs and neck, and much shorter hind legs; only the front legs possess knees. Al-Jahiz, in his *Book of Animals*, gives at length details of the origin of the giraffe. According to him, during the summer heat, a great number of ferocious beasts and wild animals had assembled, on the shore of a vast stretch of water situated at the edge of Nubia. Of the matings which resulted some were sterile, others gave birth to products very strange in form and appearance, the giraffe among others. This animal has a forked foot; its back is depressed and slopes to the rear, because its hind legs are very short. The origin of the giraffe has given rise to numerous discussions. One must note that the Nubian panther attains great growth, while the camel of this country has a meager form and small legs. Young Arabian camels were cited as outstanding analogous examples of such reproductive methods among the animals native to Kerman or to other provinces of Khovacan (*Camelus bacterianus*) for they give birth to species called *bokhti* or *jemmazeh*. There has never been a mating between a camel and a *bokhti* female, and the better products of that species result from a crossing of the large camel having two humps with a young female Arabian camel; but the kinds called *bedjavi* and *mahari* could produce also *bokhti* camels. A long account of the giraffe is found in the great work on animals by Aristotle; this author explains the functions of each limb of the giraffe and of every animal in general. We have borrowed from him in our book of *Questions et experiences* everything that is worth knowing on the subject.

The following quotations from Bartholomew the Englishman (Bartholomaeus Anglicus), who lived in the first half of the thirteenth century, show no scientific advancement over those of the tenth century Arab. Sometime between 1230 and 1240 A.D., Bartholomew wrote *De proprietatibus rerum*, which soon became one of the most popular textbooks of medi-

eval Europe. The quotations are from an English translation printed at Westminster about 1495. The influence of Pliny is obvious:

. . . Li. °/VIII.°°/ ca°. XVIII Plinius spekyth of y^e^ lyon and sayth y the lyon is in moste gentylnesse and nobilyte whan his neck & sholders he helyd wyth heer & mane / And that he is gendryd of the parde lackyth that nobylyte / The lyon knowyth by smelle yf the pard gendryth w the lyenesse; and aresith ayenst the lynesse that brekyth spousehede: & punyssheth her full sore but yf she wasshe her in aryver & thenne it is not knowen to the lyon /

Hiena is a cruel beast lyke to y^e^ Wulfe in devourying & gloteny and resith on deed men: and takyth theyr bodyes out of erthe & devouryth them / And hath therfore that nam Hiena of Hiendo / for desyre he resyth to his proye wyth open mouth & voys / It is hiskynde to change Sexus / For he is now founde male and now female: & is therfore an unclean beast as Isyder saythe / And comyth to hous by nighte and feyneth mannys voyce as he maye / for men should trowe that it is a man. Libro VIII°. /capto: XXXI°. Plini spekyth of this beest & sayth. that in Hiena is eyther kynde / for it is sayde one yere male and a nother yere female / And she bryngth forthe her broode wythoute male as the commom people trow /

. . . / And this beest gendryth wt a lyonesse of Ethiopia and gendryth on her beest that is moost cruell / And folowyth the voys of men & and of tame beests and hathe many rowes of teeth in every syde of the mouthe.

Another account of the same hybrids was written by Ser Brunetto Latini some time between 1264 and 1267. Latini, born early in the century at Florence, was exiled to France in 1260. He wrote in French *Li livres dou trésor*, which shortly acquired great popularity. He died in Florence in 1295. His description of the hybrids well illustrates the little progress made in the preceding 1,200 years:

The hyena is a beast which is at one time male and at another female, and it inhabits the cemeteries of dead men, and mangles and eats the bodies of the dead. And the bone of its back is so hard that

it cannot bend its neck, and if it enters any narrow place it can only get out by backing out, but rather they say that it does not return whence it enters. And it haunts dwellings that have stables, and imitates the voice of people and thus often deceives men and dogs and devours them.

And many say that in its eyes there is a stone which is of such virtue that if a man have it under his tongue he can foretell the things that are to be. And because that animal which touches its shadow cannot move from that spot, the ancients say that this beast is filled with enchantment and magic art.

And you must know that in Ethiopia this beast mates with the lioness and engenders a beast that is called "coccie" or true "corococte" which imitates, likewise, the voice of man, and in its mouth it has no gums nor separate teeth like other animals, but it is all one tooth and closes like a bag [purse].

Chapter 41:

The other kind of lions are engendered from a beast which is called pard: and these lions are without hair and without nobility, and are counted among other wild beasts.

It should be noted that at about this time Albertus Magnus rejected the stories of the lionesses' adultery with the pard, but Thomas of Cantimpre retained the slander. From the translation of Konrad von Megenberg, *Buch der Natur*, written in the first half of the fourteenth century (Book III, Chapter 381):

The leopard is an animal born from the lion and the pard. The female is stronger than the male and swifter. . . . Many say that the leopard and the pard are one animal who has two names.

The word "hybrid" is used in the exact sense given it by Pliny (Bk. III A, Chapter 34):

Concerning Hybrids

"Ibrida" is a four-footed animal and is of double descent (*Zwidorn*) for it comes from wild swine and from tame, the same as a mule

comes from a horse and an ass. For this the Germans have no special name, but one may call it swine of double origin (*Zweilahtigerz*) just like a *tyadrus* which is a goat-sheep, which is born from a sheep and a he-goat, and *muscus* comes from a she-goat and a ram. That may be called in German a sheep-goat.

During the next two centuries accounts of hybrid swine, mules, and leopards reappeared in many texts. These need not be quoted here, for they differ in no essential from their predecessors. Nicolaus Perottus (1430-1480), Archbishop of Siponto, gave a detailed description of these three hybrids in his *Cornucopiae* as did Grapaldus in *De partibus aedium* (1506) and Maffejus in *Commentiarum Urbanorum* (1506). while Jovannis Ravisius Textoris in *Epitheta,* Parrhisiis, 1521, told of the lioness-panther cross. There must have been something very pleasing in the story of the King of Beasts being betrayed by his own wife. Perhaps it gave satisfaction to those not of the Royalty, for the story lasted into the eighteenth century, and was included by Hans Friedrich von Fleming in *Der Volkommene Deutsche Jäger,* Leipzig, 1719. From page 83:

> When the lion is incapable of concupiscence because of the great heat of the sun, the lioness, on the other hand being very lustful, often cohabits with animals of other species.

In spite of the fact that great progress was made during the fifteenth and sixteenth centuries—a new world was discovered and explored while many ancient taboos slowly disintegrated —scientific skepticism remained noticeably absent from the work of the philosophers and naturalists. Hearsay evidence was still accepted at face value, and almost any marvel was believed if it was reported to have occurred in a distant country. Myth, tradition, and authority still ruled. In no field of endeavor, perhaps, are the low scientific standards of the time illustrated as well as in that of animal hybridization. The

medieval records of absurd crosses passed unquestioned, and every stillborn foetus, whose abnormality was not assigned to the prenatal influence of the mother's imagination, was looked upon as evidence of her bestiality. From the middle of the sixteenth century to the middle of the eighteenth, innumerable accounts of these fantastic hybrids were written, some by the greatest naturalists of the time. It will be impossible, in a work of this scope, to treat the subject adequately. Only a few outstanding samples will be quoted to illustrate this mass of biological literature.[8]

The first example of these descriptions of hybrids is taken from the famous *Nomenclator* of Conrad Gesner. Gesner was the outstanding zoölogist of the sixteenth century. The following extracts are from the edition of 1560. From p. 68—

One is the panther of the Greeks, only of male descent, which is included with the wolves, others indeed would be that deer-like wolf which is commonly called lynx: others are dog-like (as Theodorus and Niphus translate from Aristotle) which the Greeks still commonly called panther, the Arabs the Armenian wolf, the Turks the cicalum, a menial animal smaller than a wolf, and in other ways greatly degenerated. The same animal is called panther and lycopanther, etc. Those who describe this dog-like wolf imply its birth from a union of dog and wolf: Such an animal we often see, just like a domestic dog, with little likeness to a panther. Those indeed who named the lycopanther made it the offspring of a wolf and panther; Those who named the leopard, made it the offspring of a lion and panther.

The hyena is described (page 78):

That animal composed equally of wolf and dog which in Ethiopia is called Crocottas (according to Agatharchides) receives this name.

[8] These records were summarized in a number of contemporary books on natural history, miracles of nature, causes of monsters, etc. Modern geneticists who wish to investigate this phase of the subject would do well to consult Porta (1558), Cardan (1557, 1558, 1560), Columnae (1592), Bauhin (1614), Zacchias (1621), Del Rio (1633), Licetus (1634), Fabri (1677), Paullini (1685), Schurig (1732), and Haller (1757-1766).

However, it is both more savage and much more heavily made and also has larger feet. Admirable for its strength, excelling in strong teeth and stomach (digesting everything) it crushes, splits, devours easily all kinds of bones and consumes incredible mixtures. It is said that they imitate human speech, although in truth they do not deceive us: and they devour him whom they call by name at night, approaching him just as a man.

The hyena conceives by a wolf and brings forth Onolysum, as it is pronounced (it is written Monolycum), which lives not in a herd but as a solitary, and wanders among men and flocks, as a Greek wrote recently, who attributes to him indeed rough thick hair: and without neck vertebrae and stiffened in one upright bone, just as Pliny and also Solinus and even Aelianus write about the wolf, and others about the lion.

From page 122:

Concerning the Second Order

The Hinnulus is born of a bull and a mare. We see many, says Scaliger. We had two some time ago; now one young female between whose ears two bony lumps the size of seed-acorns protruded themselves as native rudiments of the paternal forehead. They say superior teeth are indeed lacking in this offspring. It is frequently defective in this respect, because a lower jaw which protrudes is superior; which is noticed in many fish. Two-thirds of these things were said by Gabolis and Arverins.

This last hybrid described by Gesner, the hinnulus, born from the union of a bull and a mare, deserves further treatment. There is nothing remarkable in the fact that this monster was cited as an authentic instance of hybridization for well over two hundred years. It only illustrates the scientific standards of the time. Many of the descriptions, however, seem to be independent eye-witness accounts from several different countries, and no one ever seems to have doubted the creature's existence. As a chronological arrangement of these records forms an excellent cross-section of sixteenth, seventeenth,

and even eighteenth century hybrid lore, they will be quoted here in full, although of course they are without intrinsic value. The first account is taken from Porta's *Magia Naturalis* which appeared in 1558 and passed through many subsequent editions. The quotation is from the English edition, *Natural Magick*, London, 1658. From Bk. II, ch. 9, page 39:

But there is a more common kind of *Strong Mules gendered of a Bull and an Ass*, which is a fourth sort of Mules, found in Gratianopolis, and called by a French name Jumas. Gesner reports that at the foot of the Hill Spelungus, in Rhetia, was seen a Horse gendered of a Mare and a Bull. And I myself saw at Ferraria, certain beasts in the shape of a Mule, but they had a Bull's head, and two great knobs instead of horns: they had also a Bull's eyes, and were exceedingly stomackful, and their colour was black: a spectacle, wherewith we were much delighted. I have heard, that in France, they be common: but I could see none there, though I passed through the whole country.

Cardan in *Contradicenta Medica*, Paris, 1565, refers to this hybrid briefly, from Bk. II, ch. 6, p. 8:

Third, the sons of bulls and mares are very robust and brave: resembling their fathers.

Zacchias in *Questiones Medico-legales*, Rome, 1621, also describes the cross briefly. From Bk. VII, Tit. 3, Quaes. I (p. 584, ed. after 1688):

In order that this might become more apparent, we choose an animal born from parents of different species, as, for example, a "cud-chewing" father and a solid-hoofed mother, such is a mule born from a bull and a mare: now always from such parents, you will see that a solid-hoofed offspring is born.

Nieremberg (1635) mentions these animals in his general account of hybrids (see p. 40), and Leger in his *Histoire du Vaudois*, Leyden, 1669, describes them at some length. From pp. 7-8:

Among the domestic animals, there are only the *Jumarres* which I find are entirely unknown in all these northern countries. This animal is born from a bull and a mare or of a bull and a she-ass: The first mentioned are larger and are called *Baf* and the latter are smaller and are called *Bif*: The former have an upper jaw, nearly like the pigs, but so that the upper teeth are an inch or two further back than those in the lower: the latter on the contrary have a longer lower jaw, nearly like that of the hares or rabbits but so that the teeth may graze in the pasture where the grass is so long that they cut it with their tongue: except for the difference in the length of their jaws, you see their form in the following figure, and you see how they have the skin and tail of a bull and even little elevations in the place of the horns: in all other characters they take after the horse or the ass. Their strength is inconceivable considering their size, they are smaller than he-mules, they eat little but they devour the distance. With such a *Jumarre* I covered forty-five miles on the thirtieth of September, entirely through mountains and covered it much more easily than on horseback.

Venette discusses the cross in *La Generation de l'homme ou Tableau de l'amour conjugal*, Amsterdam 1687. From Pt. 3, ch. 8. (p. 536, ed. of Cologne, 1702)—

There are again other types of monsters which are formed through the mixing of different species. The histories which we have on this subject make us believe that the thing is possible. The *Hippotaure*, which the Cardinal of the Comitibus sent from France to Italy and which he subsequently gave to the Cardinal Scipio Borghese, is not just a story told to please. All Rome saw it and admired it for a period of thirty-two years, after which it died, its teeth failing. It had the head of a bull but the rest of the body was like a horse. I understand that in Auvergne and elsewhere, this type of animal is engendered by a horse and a cow.

John Locke (1690), in the famous *Essay concerning human understanding*, stated that there were many bull-mare hybrids in the world (see p. 58), and Thomas Shaw, the missionary,

claims to have found an ass-cow hybrid in Algiers. Shaw described it in *Travels or Observations relating to several parts of Barbary and the Levant*, London, 1710.

To the mule we may join the kumrak, as the Algerines call a serviceable beast of burden begot of an ass and a cow. That which I saw at Algiers, where it was not looked upon as a rarity, was single hoofed like an ass, but distinguished from it in having a sleeker skin with the tail and the head (though without horns) in fashion of the dams.

The description of the bull-ass hybrid in Bourguet's *Lettres Philosophiques*, Amsterdam, 1729, seems to be taken in great part from Leger. From Lettre IV, p. 161—

Nothing seems to me more calculated to prove the reality of the action of the pure extract of the bodies of the male and the female on the offspring than the example of the young ones who have been produced by animals of different kind. One sees in Piedmont *Jumarres* which they divide into two kinds: the first, which comes from a she-ass and a bull, is called *Bif*, and the second, which comes from a mare and a bull, is called *Baf*. These animals, which really are mules and horses, because the young belong to the species of the female, bear nevertheless marks of the male, that is to say, that they have the forehead a little uneven in the spots where the bulls have horns, their one jaw is a little shorter than the other and their tail holds something like that of a bull. As for the he-mules which are common in Piedmont and in all of the southern countries of Europe: since the jackass does not differ as much from the horse as the bull does, the species are more blended in the young: and yet, the marks of the male are very obvious in them, although the he-mule is a horse and not a corrupted jackass, as one can convince himself in examining it carefully. That twofold species of monsters proves clearly that the primitive organized corpuscles are in the eggs of the female and not in the sperm of the males and that the liquid mixed with that of the female acts on the preëxistent organized body for its own growth and first nutrition. The children, born of a white father and black mother or of a white mother and a black father, prove absolutely the same thing with reference to men.

Even as late as the middle of the eighteenth century Buffon (*Histoire des Animaux*, ch. 12) believed that the accounts of this hybrid should be carefully investigated. It is interesting to note in this connection that a hornless cow is called a muley-cow and that this term has been in use ever since the sixteenth century.

The hybrid issue of *Equus equus* × *Bos taurus* were not the only samples of inter-family crosses which the philosophers accepted as authentic. John Locke stated that he saw a creature descended from a cat and a rat (page 58), while the rabbit-cat hybrid, still described periodically in our rural sections, was reported from many countries. There were traces of skepticism, however, and John Morton (1712) went to some trouble to explain that a Manx cat need not have had a rabbit for a father. Morton, however, wrote toward the end of this period, a time when doubts were growing. Far more typical is the work of the great agricultural writer, Konrad Heresbach, whose *Rei Rustica* appeared in 1570. This work was translated into English by Barnabe Googe, Esq., and issued as *Four Bookes of Husbandri*, London, 1586. Novel methods of engendering are described, and the account of the hybrid between the wild boar and the female camel is worthy of Aristotle himself. From page 127:

The Camels

He engendreth backward, as the Elephantes, Tygers, Lions, Connies, and such other, whose instruments grow backwards: when they mean to go to rut, they seek the secretest and desartest places that may be: neither may a man at any time come neare them, without great danger.

. . . . . .

And the female Camell of *Bactria*, feeding upon the Mountains amongst the wild Boares, is oftentimes breamed of the Boare, and conceaveth. Of the Boare and the shee Camell, is engendred the Camell of the two iumpes upon the backe, as the moyle is of the Asse,

and the Mare, and in divers thinges resembleth his sire, as in bristled heares, strength, and not fainting in the mire, but going lustily through, and carrying dooble as much as other Camelles, as the same authour sayeth. . . . There are a kind of them called Camelleopards, that have the resemblance of two divers beasts, the hoofes and hinder legges like an Oxe, his forelegs and his head like the Camell, the neck like a horse being flecked white and redde.

Johannis E. Nieremberg wrote *Historia Natura* in 1635. The following excerpt is from the edition of 1675 (Bk. V, ch. 24, p. 91a)—

Concerning False or Bigeneric Animals

Having mentioned these false and bigeneric animals, it is necessary that we describe at least the more famous of them. B. Eugenius the Younger, President of Toletum, collects some of them in this song:
These are the ones which come from an unequal bigeneric marriage.
The steed generates the hinney when he is united to the little she-ass.
The mule is created from Arcadian asses with a mare for a mother.
Titirus arises from sheep with a goat for a parent.
The she-goat bears a muflone from a wether's blood.
From wild boars and a sow a bristly hybrid is born.
But a he-wolf and a young she-dog form, by coition, a wolf-dog (*lyciscam*).
Others can be added. An *alphet* or *alpheil* is generated from a lioness and a leopard. Arcadian dogs and *Hircani* from the dog and the tiger. The story is that the Arcadian dogs were born first from dogs and lions. . . .

Dogs conceive even from a he-wolf. Laconian dogs called *alcopecides* are born from the wolf and the dog. There are some who think a wolf is dog-like and is born from a she-wolf by contact with a male dog. Solinus declares that the ignoble race of lions comes from lionesses and pards. Leopards from a pard and a lioness. Philostratus writes that a lioness conceives not by a pard but by a she-pard (?) (*pardali*). Since a lioness conceives by a pard and bears offspring like herself in body but unlike herself in spirit, it must be asked whether a she-pard or a she-panther conceives by a lion and thus bears a manly (*mas-*

colosum) offspring. Didymus teaches that the Bactrian camel is fecundated by wild boars while they are pasturing together. Pliny and Solinus say that the crocuta [an unknown wild animal in Ethiopia, perhaps the hyena] is born from the Ethiopian lioness and hyena. Francis, King of the Gauls, had a horse with the hind part of its body born from a deer-like animal, as if born from a stag and a mare. Bellonius notes that, among the Raetians, animals are born from the coition of a she-goat with a ram, which have the fore parts of a sheep, the hind parts of a goat. Oppianus tells of a kind of wolf born from a he-wolf crossed with a she-pard and a she-panther. A mule is born from a he-ass and a mare; another, called a hinny, from a stallion and a she-ass. From a mare and tamed wild asses mules are generated which are very swift in running. A fourth race of mules is produced by a she-ass and a wild ass, a fifth by a she-ass and a bull. All bigeneric things become like their mother: they seem to receive more from the mother, especially in respect to the shape and the form of the body.

Numerous hybrids were also reported among the birds. Willughby (1676) stated that these were all sterile (*Ornithology p. 12*). Des Serres (1603) described the crosses of diverse varieties of pigeons. The most frequently described hybrid, however, was the cross between the common barnyard chicken and the pheasant. Cardan gave an account of this mongrel as early as 1557 (*De rerum varietate* Bk. 7, ch. 36 pp. 371-372). The great William Harvey, who discovered the circulation of the blood, cited an analogous hybrid as evidence that both parents contributed to the formation of their progeny. From *Generatione Animalium*, London, 1651, Exer. 33, p. 142—

The medical writers with propriety maintain, in opposition to Aristotle, that both sexes have the power of acting as efficient causes in the business of generation: inasmuch as the being engendered is a mixture of the two which engender: both form and likeness of body, and species are mixed, as we see in the hybrid between the partridge and common fowl.

Fabri described the hybrid in *Tractatus duo*, Norembergae, 1677 (Tract. I, Bk. 5, prop. 67, pp. 182-186), and Richard Bradley stated in *The Country Gentleman's and Farmer's Director*, London, 1732 (p. 30), that:

> One may now produce a Cross-Strain of Fowls, between a Cock Pheasant and the Hens of common Poultry, if we keep a Pheasant Cock in company with six or seven Hens, in a place where there can be no other mixture: the Fowls bred from there will be of a delicate Flesh.

George Edwards described and pictured a bird which he assumed to be a cross between the turkey and the pheasant. This was as late as 1760, yet the *Philosophical Transaction* accepted his article and published it in volume 51 (p. 833). Buffon in his *Opera omnia*, issued ten years later, accepted this hybrid as authentic.

Toward the latter end of the preceding century, Leewenhoeck described a real instance of variety crossing in rabbits in one of his letters to the Royal Society. This contribution was included in the paper, *Epistola de generation Ranarum* and published in the *Philosophical Transaction* of October 1683 (Vol. XIII, pp. 347-355). The quotation is from pp. 349-350.

> . . . Many of our *Neighbours* either for their pleasure or profit, keep tame *Rabbits*, which are long eard, ordinarily of a white colour, but sometimes of Blew, Black, and Pyed; those that would make a profitt of these *Rabbits* by causing them to bring gray young ones, which in the fore part of the year may be sold for a wild kind; get a *grey Male*, such as are ordinarily found on our *sand hills*, to put to their female: The *Breed* that comes from hence always takes the gray colour of the *Male*, and it has never been seen that any of the young has any *white*, or other coloured hair than *gray*, there withal they are never so bigg as the *Dam*, nor have so great ears, nor are so tame, but of a wilder kind.

4. HUMAN HYBRIDS

The thought of human beings crossbreeding with other forms of life has always intrigued a number of people. Indeed there is little doubt but that bestiality was at least a sporadic practice among many tribes of primitive herdsmen. The Hebrews were expressly forbidden the practice under penalty of death (Lev. 18:23-24, 20:15-16, Ex. 22:19), yet the language of the commandment seems to imply that bestiality was an ancient Canaanite custom. The general aspirations of mankind were much higher, however, and the myths that have come down to us from the earliest civilizations contain many accounts of miscegenation between gods and mortals. The leading families of ancient Egypt and Babylonia, as well as those of Greece, Rome, and Scandinavia, traced their ancestry back to the philandering of some of their tribal gods. Even Socrates, while on trial for his life, solemnly affirmed his belief in demigods and Alexander the Great certainly fostered the idea that there was more to his birth than King Philip of Macedonia suspected.

That great men were descended from the gods was once a universal belief. The growth of monotheism, however, introduced complications and the "men of renown" of the most ancient myths were apt to degenerate into "wicked giants." The second and fourth verses of the sixth Chapter of *Genesis* actually show this transition.

> 2. That the sons of God saw the daughters of men that they *were* fair; and they took them wives of all which they chose . . .
>
> 4. There were giants in the earth in those days; and also after that, when the sons of God came in unto the daughters of men, and they bare *children* unto them; and the same became mighty men, which were of old, men of renown.

More details of these matings are given in the apocryphal *Book of Enoch,* which was probably written in the first or

second century before Christ by some Sadducee living in northern Palestine. This work was never accepted as canonical, yet it had marked effect upon early and medieval Christianity. Hildegard of Bingen especially showed its influence. From I Enoch 12:4-6:

Enoch, thou scribe of righteousness, go declare to the Watchers of the heaven who have left the high heaven, the holy eternal place, and have defiled themselves with women, and have done as the children of the earth do, and have taken unto themselves wives: "Ye have wrought great destruction on the earth." 5. And ye shall have no peace or forgiveness of sin and inasmuch as they delight themselves in their children. 6. The murder of their children they shall see. . . .

I Enoch 15:3:

Wherefore have ye left the high, holy and eternal heaven, and lain with women, and defiled yourselves with the daughters of men and have taken to yourselves wives, and done like the children of earth, and begotten giants as your sons?

The eighty-sixth chapter gives an account of these same happenings in figurative language. The symbolism needs no explanation.

And again I saw with mine eyes as I slept, and I saw the heaven above, and behold a star fell from heaven, and it arose and ate and pastured amongst the oxen. 2. And after that I saw the large and black oxen, and behold they all changed their stalls and pastures and their cattle, and began to live with each other. 3. And again I saw in the vision, and looked towards the heaven, and behold I saw many stars descend and cast themselves down from heaven to that first star, and they became bulls among the cattle and pastured with them. 4. And I looked at them and saw, and behold they all let out their privy members, like horses, and began to cover the cows of the oxen, and they became pregnant and bare elephants, camels and asses.

Lactantius (260-340 A.D.), one of the early Christian fathers, also described this mating. According to his account the offspring showed traces of the natures of both parents:

Chap. XV—OF THE CORRUPTION OF ANGELS, AND THE TWO KINDS OF DEMONS.

When, therefore, the number of men had begun to increase, God in His forethought, lest the devil, to whom from the beginning He had given power over the earth, should by his subtility either corrupt or destroy men, as he had done at first, sent angels for the protection and improvement of the human race; and inasmuch as He had given these a free will, He enjoined them above all things not to defile themselves with the contamination of the earth and thus lose the dignity of their heavenly nature. He plainly prohibited them from doing that which He knew they would do, that they might entertain no hope of pardon. Therefore, while they abode among men, that most deceitful ruler of the earth, by his very association, gradually enticed them to vices, and polluted them by intercourse with women. Then, not being admitted to heaven on account of the sins into which they had plunged themselves, they fell to the earth. Thus from angels the devil makes them to become his satellites and attendants. But they who were born from these, because they were neither angels nor men, but bearing a kind of mixed nature, were not admitted into hell as their fathers were not into heaven. Thus there came to be two kinds of demons; one of heaven, the other of the earth. The latter are the wicked spirits, the authors of all the evils which are done, and the same devil is their prince.

The *Clementine Homilies*, an anonymous work of the third century which was falsely assigned to Saint Clement of Rome, gives a somewhat different description of these hybirds. From Bk. VIII, ch. 15:

The Giants

But from their unhallowed intercourse spurious men sprang, much greater in stature than *ordinary* men, whom they afterwards called giants: not those dragon-footed giants who waged war against God, as those blasphemous myths of the Greeks do sing, but wild in manners and greater than men in size, inasmuch as they were sprung of angels; yet less than angels as they were born of women. Therefore God, knowing that they were barbarized to brutality, and that the

world was not sufficient to satisfy them (for it was created according to the proportions of men and human use), that they might not through want of food turn, contrary to nature, to the eating of animals, and yet seem to be blameless, as having ventured upon this through necessity, the Almighty God raised manna upon them, suited to their various tastes; and they enjoyed all that they would. But they, on account of their bastard nature, not being pleased with purity of food, longed only after the taste of blood. Wherefore they first tasted flesh.

Mere racial crossings within the genus *Homo* seem much more prosaic than the begetting of demons, yet even these crosses have given rise to legends, which still persist. The following excerpt from Aristotle shows how old some of our folk tales really are. Many novelists and playwrights have used such instances as the following as themes for their melodramas. If black skin in man were conditioned by a single sex-linked recessive gene, the following incident would be possible. From *De Generatione Animalium*, Bk. I, Ch. 18:

Further, children are like their remote ancestors from whom nothing has come, for the resemblances recur at an interval of many generations, as in the case of the woman in Elis who had intercourse with the Æthiop: her daughter was not an Æthiop but the son of that daughter was.[9]

Antigonus tells the same story in *Historia Mirabilium*. From Chapter CXXII:

A woman of Elis, impregnated by an Æthiopian in adultery,

[9] Aristotle repeated this story in the *Historia Animalium*, Bk. 7, ch. 6 . . . "While children mostly resemble their parents or their ancestors, it sometimes happens that no such resemblance is to be traced. But parents may pass on the resemblance after several generations, as in the case of the woman in Elis, who committed adultery with a negro; in this case it was not the woman's own daughter but the daughter's child who was a blackamoor." Jerome Cardan told the same story eighteen hundred years later (1565). From *Contradicenta medica*, Bk. II, Tract 6. §17—"Likeness appear even after many generations in Elis, when a woman conceived from an Æthiopian and bore a white daughter; the daughter, however, bore a son similar to an Æthiopian, certainly therefore the original seed was the cause of the blackness and it was proper for the offspring to be black."

gave birth to a white daughter and from the daughter was born an Æthiopian.

When Pliny, retold the story there were some variations and additions. From Pt. I, Bk. 7, Ch. 12:

. . . Ye shall have women bring all their daughters like to their fathers, and contrariwise, their sonnes like the mothers. The example is notable, and yet undoubted true, of one *Nicaeus,* a famous wrestler of Constantinople, who having to his mother a woman begotten in adulterie by an Æthyopian, and yet with white skin, nothing different from other women of that country, was himselfe blacke, and resembled his grandsire, the Æthyopian aforesaid. Certes, the cogitations and discourses of the mind make much for these similitudes. . . .

Plutarch (46-125 A.D.) included a version of this story in a work which bore the appropriate title, *Concerning those whom God is slow to punish.* In section 21 he described discontinuous inheritance and cited a number of hereditary peculiarities which appeared in alternate generations. The reappearance of the Ethiopian traits is reported as follows:—

For . . . the warts and moles and freckles of parents, not seen upon the children of their own begetting, many times afterwards appear again upon children of their sons and daughters; and . . . the Grecian woman that brought forth a blackamoor infant, for which she was accused of adultery, proved herself, upon diligent inquiry, to be the offspring of an Ethiopian after four generations. . . .

The resemblance of children to their more distant ancestors was noted in classical times and described by writers more reliable than Pliny. Galen himself called attention to this occurrence, and he cited the fact in his attack upon the superstitions connected with prenatal influence. In showing that the appearance of the offspring was not controlled by the passing whims of the pregnant mother, he stated (Vol. 14, p. 253, edition of 1821): "For offspring resemble not only their parents, but even certain grandparents," which proved, he

believed, that prenatal influence could no longer be called upon to explain the freaks of heredity.

An interesting, if fantastic, record of a human variety cross was written by Thomas Bartholini in the seventeenth century. In the *Historia anatomicarum rariorum* (1657) he records a human cross reminiscent of Pliny. This incident was quoted in all seriousness by Wahlbom (1746) and Haartman (1751), both pupils of Linnæus. From Century IV, History 5:

Hybrid

An Æthiopian artizan, detained in the Hafnian prison, was fired with love for a slave girl, and secretly raped her. Thence she became pregnant, and in due time brought forth a male child which resembled its mother inasmuch as the skin of its entire body was white, but the penis alone was black and showed the father's lineage. I assign this on the whole to the imagination[10] of the mother whose seizing upon the desired part more vehemently with a set mind impressed the color of the same on the fœtus. Other fœtuses of mixed colors may be generated from Æthiopians and white, which is often seen by us, if, in fact, each sex has a regulated share in generation.

[10] It was generally believed that the imagination of the mother need not always work to the detriment of the child. Black skin could become white as well as white skin black. Such an instance is described by Heliodorus about the year 400 A.D. in the first romance ever written, *The Adventures of Theagenes and Chariclea.* Persena, the black Queen of Æthiopia, gave birth to a white daughter although she had been faithful to her black husband. In the *dénouement* she explains to her daughter what had happened (tr. by Rowland Smith):

But when at last I brought you forth, a white infant, so different from the Æthiopian hue, I was at no loss to explain the cause, since, in the embraces of your father, I had kept my eyes fixed on the picture of Andromeda, whom the painter had represented just unchained from the rock, and my imagination had communicated her complexion to my unhappy offspring.

Thirteen hundred years later a like instance was described in *The British Apollo,* a journal published in 1708. The following passage, an answer to a query about Jacob's piebald cattle, is on page 467 of the third edition (1726).

A. The flocks conceiv'd, and brought forth cattle of the colours above-mention'd, by the powerful efficacy of a fix'd imagination; which generally produces effects in the conception answerable to the fancy of the agents in the act of generation; and does often work the "form ingendred" into a perfect similitude with the prevalent idea of the generator: Among a thousand proofs of which, the celebrated story of the "Spanish" Lady is remarkably particular, who by constant and intent.ve views of a tall negro's picture, which hung directly opposite to her beds-feet, conceiv'd, and was deliver'd of a Negro child, which, but for a physician's learning, and judicious discovery of the cause, had cost the innocent Lady both her life and reputation.

Joachim Becher (1669) in *Physicae subteraneae* included a description of the inheritance of skin color in man, in his account of hybridization in the animal kingdom. He also noted some of the consequences of bestiality. From Bk. I, Sec. IV, Chap. IV, N. 17-21, (p. 214-216, Edition of 1681)—

. . . for a mare, by the first conception made with an ass, bears indeed a mule, yet in a second conception when a horse is born, and as manifestly for this reason remarkable relics are discovered concerning the earlier idea of an ass, when such horses are usually praised for their endurance and other like qualities; and we see this occur in certain other animals, also doves especially, for often at first young are hatched from a black dove and a white dove, some of which are plain black, others plain white, and later, in truth, if the black ones mate with the black and the white ones with the white, then at length it appears that variegated young are born, and this even now is imitated to a certain point in the natural grafting of trees, for when red and white fruits are combined, a mixture of colors does not appear until the second grafting. Indeed also in man examples of such a thing are not lacking, for if some rather old Spaniard or Portuguese with a black face, takes a wife of a white color, at first indeed the children are white and like the mother in face and nature if the feminine face predominates, but afterwards when they mate again with white ones they produce offspring which are blackish, the descendants being unquestionably like their grandfather as much in nature as in face, and sometimes this is even found to occur in the third generation. Helmontio as a witness recounts these things in *Alphabet of nature*. There are also various reports saying that in the feminine phantasy bears and apes mate with women, nevertheless the women are permitted to adjust the particles of this bestial seed destined for the forming of wild beasts to the contrary human condition and to generate a true man, although hairy and of exceptional strength, and there are also contrary examples whereby men (if they may be called men) have mated with the females of animals, with a cow among others, which bore not a man but a repulsive monster beyond human imagination, for on the contrary the cow struggled against the nature of the seed with its natural inclination for human form, whence the product showed

a figure taken partly from the man and partly from the cow, and everything of its life proved the necessity and power for forming a fœtus. And so, in truth, let it not be our proposition to deal with extraordinary particulars concerning the generation of animals, since what we have said so far has been said without the possibility of making any comparison between an animal and a mineral mixture.

Becher's reference to bestiality shows that his views on the subject were in no way original. In the seventeenth century it was believed that mankind could cross with animals either in phantasy or in actuality. Women with perverse imagination could have bear-like progeny just as Persena could have a white daughter (See page 47) and men supposedly could beget offspring upon animals. Both men and women had actually copulated with beasts from the earliest times, and while such acts were often looked upon as criminal (Lev. 18:23-24, 20:15-16, Ex. 22:19), they were sometimes tolerated and even invested with a certain religious significance.[11] The celebrated instance in *The Golden Ass* of Apuleius is but one of many such perverse acts, for the pagan women seem to have been on the whole as bestial as the men. One of the earliest accounts of such bestiality is in a lost fragment of Pindar (500 B.C.) which can be reconstructed, however, from several citations. The event was said to have happened in Egypt. A

[11] In many instances the animal was a metamorphosed god (Europa and the Bull, Leda and the Swan, etc.). The Minotaur, however, was thought to have arisen through an act of pure bestiality. In the *Images* of Philostratos (190-247 A.D.), a picture of the building of the hollow cow is described, the cow which Dædalus made for Pasiphaë, the wife of Minos. From Bk. I. ch. 16:

> Pasiphaë is in love with the bull and begs Dædalus to devise some lure for the creature; and he is fashioning a hollow cow like a cow of the herd to which the bull is accustomed. What their union brought forth is shown by the form of the Minotaur, strangely composite in nature. . . .
>
> Pasiphaë outside the workshop in the cattlefold gazes on the bull, thinking to draw him to her by her beauty and by her robe, which is divinely resplendent and more beautiful than any rainbow. She has a helpless look—for she knows what the creature is that she loves—and she is eager to embrace it, but it takes no notice off her and gazes at its own cow. The bull is depicted with proud mien, the leader of the herd, with splendid horns, white, already experienced in love, its dewlap low and its neck massive, and it gazes fondly at the cow; but the cow in the herd, ranging free and all white but for a black head, disdains the bull. For its pose suggests a leap, as of a girl who avoids the impunity of a lover.

hundred years later Herodotos reported another occurrence, also in Egypt. From Bk. II, § 46:

. . . and in my time the following prodigy occurred in this district; a goat had connection with a woman in open day; this came to the knowledge of all men.

Strabo (7 B.C.) recorded this custom in his *Geography*. From Bk. 17:ch. 1, 19:

. . . There are also Hermopolis, Lycopolis, and Mendes where Pan is worshipped, and of animals a goat. Here, according to Pindar, goats have intercourse with women.

Pliny, of course, would contain some passage pertinent to the subject. From Bk. VII, ch. 3:

Of Prodigious and Monstrous Births

As for *Alcippe*, she was delivered of an Elephant, Marie that was a monstrous and prodigious token, & foreshadowed some heavie fortune that followed after. As also in the beginning of the Marsian's warre, there was a bondswoman brought forth a serpent. In summe, there be many mishapen monsters come that way into the world of divers and sundrie formes. *Claudius Caesar* writeth, That in Thessalie there was borne a monster called an Hippocentaur, i. half a man and half a horse, but it died the very same day.

In the *Greek and Roman Parallels* of Plutarch (46-125 A.D.) are two instances of bestiality. From §29 (tr. by Holland):

Aristonymus the Ephesian, sonne of Demostratus, hated women, but most unnaturally had to do with the she-asse, which when the time came, brought foorth a most beautiful maide child, surnamed *Onocelis*, as Aristotle writeth in the second book of his Paradoxes or strange incidents.

Fluvius Stellus was at warre with all women, but yet he dealt most beastly with a mare, and she bare unto him, after a time, a fine daughter named *Hippona:* and this is the goddess forsooth that hath the charge and overseeing of horses and mares: as *Agesilaus* hath set down in the third book of Italian affaires.

Ælian in *De Natura Animaliun* (Bk. 6, ch. 42), tells "the story of a she-goat loved by a goat-herder."

It will not be aside from the matter to recount the Italian story, which has come to my ears, of a deed which happened in the flourishing city of Sybaris. A youth by the name of Cratis, whose duty consisted in guarding a herd of goats, fell into an illicit intercourse with a she-goat, when he burned with the passion of desire, so that if ever it was necessary that he should enjoy love-affairs he was joined in a love embrace with the most beautiful of all the she-goats, and he considered her in the rank and place of a mistress and even used to bring her gifts not inconsistent with the desire of a she-goat. Without doubt he often offered to this same one very beautiful garlands and bindweed and the mastic-tree to be eaten, giving over to her his mouth for more fragrant kissing, and he spread for her soft, tender grass in order that she, as if a bride, might sleep more pleasantly. When, indeed, the he-goat, the leader of the herd, saw this very thing, he began to suffer because of rivalry in love and to hide meanwhile his feeling until at some time or other he could discover the goat-herder asleep, then, having summoned all his strength, he attacked the herder and crushed his head. When the story of this thing had reached the ears of the natives, however, they not only erected the youth a grave, which was not hidden, but they even named the river Cratis for him. However, it came to be the talk of men, that the infant boy conceived from his intercourse with the she-goat, had legs like a goat but the face of a man, and he had been put into the number of gods and was a certain god of the forest and a god belonging to a wooded vale. Therefore the he-goat shows that even animals suffer because of rivalry in love.[12]

In Book 7, ch. 19, Ælian further mentions other instances of bestiality:

In truth, apes with dogs' heads and goats are lustful, and some say that these have affaires with women; and Pindar seems to wonder at this. Even dogs are understood to have love affairs with women.

[12] This account of Ælian's was the source of a story told by Ludov. Coeli. Rhodigini in *Lectionum Antiquarum*. Venetiis, 1516. Bk. 25. ch. 32.

For a woman at Rome was said to have been accused of adultery by her husband: the adulterer was proclaimed in the trial to be a dog. I have indeed heard that dog-headed apes once ruined virgins and used force against them. . . .

During the unscientific centuries which followed the collapse of the classical civilizations, other strange stories of human crosses appeared. One of these recorded by Buzurg ibn Shahriyar (912-1009 A.D.) should be in our modern biological literature, for it not only illustrates the attitude of the tenth century Arabs toward hybridization, but it also shows that they recognized resemblances between man and other primates. Shortly after 954 A.D. Buzurg ibn Shahriyar wrote the *Marvels of India*, a collection of sailors' tales. The book is really a serious attempt to collect geographical knowledge in spite of its seeming preoccupation with the *outré*. From Part I, Chap. 20 (tr. by Marcel Devic):

The Crossing of Species of Animals

A person who has travelled in Zeila and Abyssina told men that one may find in the sea of Habach a fish which has the complete shape of a son of Adam, body, hands and feet. The fishermen who pass their lives in unexplored regions, on deserted shores, among islands and mountains where they never meet a living soul, sometimes discover a kind of fish with a human appearance. They mate with the females. And from this, creatures resembling men are born who can live both in the water and in the air. Perhaps these fish with the human aspect originated from the union of a man with some kind of fish,[13] a union which might have produced these beings like men; thereafter, in the course of centuries similar matings have continued. In a like manner man, in mating with the panther, the hyæna and with other terrestrial animals, produced the ape, the "nesnas" and other creatures like them. Thus the union of pigs and buffaloes produced the elephant, that of

[13] The possibility that human beings had unconsciously hybridized with fish was suggested by the ingenious if deplorable imagination of Paracelsus (*Opera Omnia*, Geneva, 1658, Vol. II-III, p. 478-479).

dogs and goats the wild boar, that of the donkey and the mare the mule. If we wished to enumerate all the results of this kind of mating, the reader would be astonished, but it would distract us from our special subject, the marvels of India.

One of the most famous of all stories of human-animal crosses can be traced, like *Hamlet*, to the great Danish historian Saxo Grammaticus. Saxo, who lived perhaps from c. 1150 to c. 1208 A.D., wrote *Historiae Danicae*, which was not printed, however, until 1533. In Book X, written about the year 1200, he describes the production of viable offspring from a human-bear cross. From p. 97 (p. 174-175, ed. of 1576):

An unusually large bear having seized a beautifully formed girl of a certain family, who had ventured into a field in Sweden with her female slaves, carried her away after beating off her companions. He bore the captive gently before him in his paws and carried her to a known hiding place in a grave. His great limbs were stirred with a new kind of eagerness, the desire of embracing rather than devouring, and he turned the plunder he had sought for mangling to the use of a wicked passion. For immediately, a lover having been transformed from an abductor, he relieved his desire by lying with her and he quenched his zeal by an abundant indulgence of his appetite for love. And in order that he might cherish her more tenderly he attacked the neighborhood cattle more violently, in frequent raids and he made her, who had hitherto been accustomed to eat only food which had been washed clean, accustomed to food spattered with blood. For so far did the species of the captive break the fierce savageness of the abductor, that the species who he used to think was eager for his blood, he thought was eager for his love and he would bring food for the one for whom he had feared he would straightway be nourishment. Where does love not penetrate or what does it not soften? Even among the savage fierceness of wild beasts, at its command the stimulus of hunger yields to the stimulus of passion. At last the owner of the pillaged herds becamed aroused at his losses and set a watch for the marauder, and contrived to hem in the wild

beast and surround him with dogs. Pursuing the fleeing bear he approached by chance the place where the girl was kept. If only the bear had covered the place with a bower! Soon the beast, surrounded by net-fighters and attacked by hunting spears was stabbed. In order that kind nature, the maker of the twofold breed, might thoroughly imbue the deformity of the marriage by the characteristics of the progeny, the monster ate the usual offspring of his kind but spared the unusual child with the blood and form of the human body. And so, a son having been born to the bear, the paternal name was given him. When the son at last discovered the truth of his posterity he demanded that fatal penalties be inflicted upon the slayers of his father. This son, Thrugillus with the cognomen Sprageleg, did not deviate from the path of virtue marked out for him by his father's courage. Ulvo, born from him, revealed his origin by his nature, showing his ancestral blood by his spirit.

This excerpt from Saxo was quoted almost word for word by Olaus Magnus (*Historia breviarum*, Amsterdam, 1669, Bk. 18, ch. 25, p. 383-385) who connected this human-bear hybrid with Danish Royalty:

. . . the son, Thrugillus Sprachaleg, departing not at all from his paternal characteristics, begot Ulfo, from whom King Sueno and other offspring of the Danish Kings were derived in a long line of succession (Saxo being witness).

This human-bear cross was cited as an authentic instance of hybridization until well into the eighteenth century, although many references to it show a certain amount of skepticism.[14] It is mentioned by Porta (1558), Bauhini (1614),

[14] Benoit de Maillet described another instance in *Telliamed: Or, The World Explained* (1748). The following is from p. 292 of the Baltimore edition of 1791:

. . . a Chinese, which author has asserted, that men were only a species of apes more perfect than those which did not speak. Though I am far from adopting this opinion, yet it is certain that from the copulation of men with them, there arise a race which has the use of speech. The same holds true in the conjunction of men with bears. Near Moscow, some years ago there was found in the cave of a bear, amidst some young bears, a child of nine or ten years of age, who had no use of speech, and who probably was begot by that animal and a woman; for if it had been a child which the bear had carried off, it would probably have had some language, unless it had been snatched from its mother's breast. Besides it is highly probable, that the bear would not have spared it so many years, if it had not been its own offspring.

Torreblanca (1623), Delrio (1633), Licetus (1634), Horstius (1664), Paullini (1685), Schurig (1732), and Haller (1757-1767). Perhaps the best example of the story's reception is to be found in the *Historia anatomicarum rariorum*, Hafniae 1657, by Bartholini. The following excerpt illustrates almost perfectly the spirit of the seventeenth century. It shows the all-pervading credulity of the time, and characteristically attempts a natural explanation of an incident that never occurred. The little story it tells is both humorous and pitiful. From Century 5, History 87,—

A Girl Born From a Dog

In our Saxo *1. 10 Hist. Dan.* it is told: A bear in a field of Sweden, seized and embraced a virgin who, pregnant, bore a son from the bear, to whom the name of "bear" was given from his parent. *Delrio 1.2. disq. Mag. quaes. 14* assigned this to a spirit, but our Stephanius *Not. ad Saxon.* wrote more rightly that the waylayer was known by the name of Ursus or Biorno. Sabellicus reports, however, *1. 7. Enn. 9 sub. Martino IV* that a famous woman bore a bear for the reason that she had seen too frequently statues and pictures of bears. Surely it is more probable that there was a rape by a real bear and that impregnation would rather follow intercourse with some animal than intercourse with a spirit, whose flesh and physical members were forsaken by life. But this embrace was rather rough, particularly with the beautiful girl resisting. I have learned from the inhabitants of Norway where there are many bears, that they love girls and that the wild fierceness of bears yields to the authority of the beautiful women.[15] It is generally known that apes stealthily seize virgins. Nor is this remarkable since they exhibit the human appearance and they are the favorites of not a few. It was told to me as the truth that in the castle of a leader of Montmorency in France, there was born from a dog to a certain woman (who had been accustomed to frolic with a dog in her bed at Melitene) a

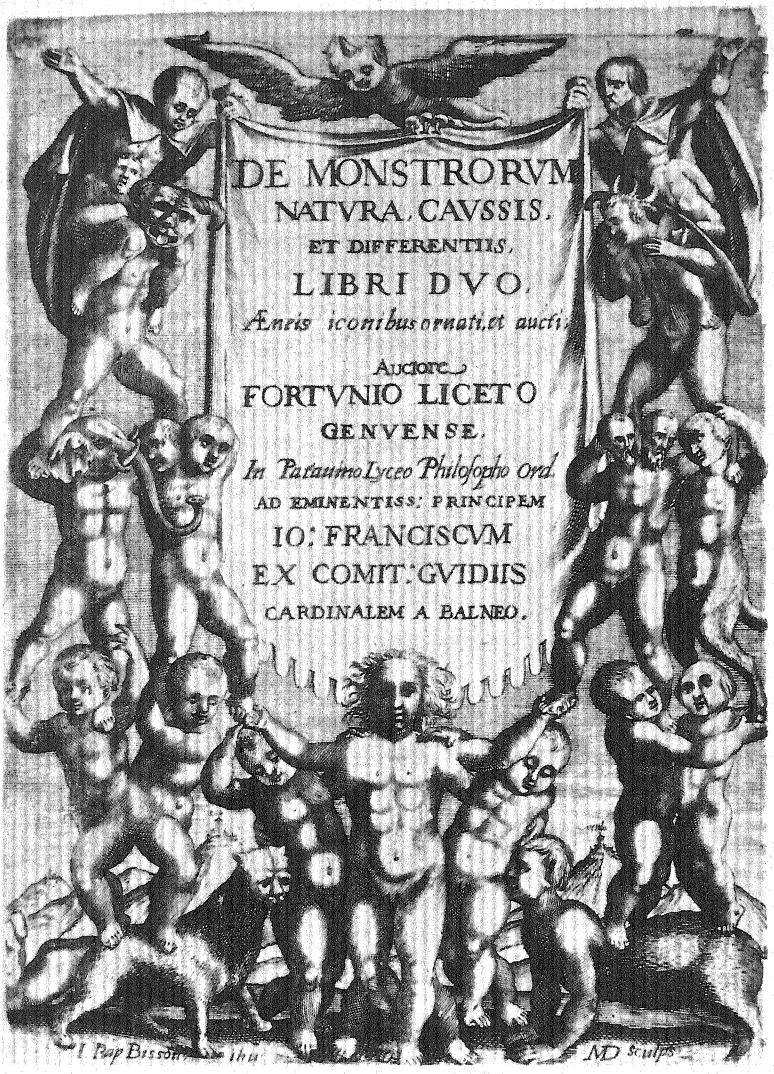
[15] A curious survival into the twentieth century of the belief that bears were made tame by women is illustrated by *The Story of San Michele*, New York, 1931, by Dr. Axel Munthe. The belief is noted on page 123.

daughter with a beautiful form and more similar to her mother than her father, for she displayed nothing canine, unless the fact that in bed she curled herself up. The mother along with the dog was assigned to the funeral pyre. But the daughter married a man who drove her to her death when during domestic fights he had charged that her father was a dog. Roccus Armensis writes in *Old Songs* that Attila was born with a dog for his father, concerning whom I have recorded many things in *de Unicornu. c.2:* At Rome under the pontificate of Alexander, a woman bore a half-dog from lying with a dog according to the writing of Jo. Langium 1.2. *Epist. Med. 9.* It outstrips my belief the fact that Mandeslous writes in *Otin. Ind.* that Macasseianas women also bring forth crocodiles.

Obviously, it would be impossible to cite all the reports of human-animal crosses which were printed during the sixteenth, seventeenth and eighteenth centuries. The stories were very circumstantial and detailed. The exact time and place were generally given, as well as the names of the erring humans and the fate of the monstrous offspring. Both men and women supposedly bred with dogs, cats, lions, goats, cattle, horses, hogs, and apes. Absurd as these accounts were, they were accepted by the majority of philosophers and doctors of medicine. Indeed the physicians, who managed to obtain still-born, defective fœtuses, were chiefly responsible for the rumors of bestiality, and many an unfortunate mother was punished because her dead infant seemed to resemble some animal. Perhaps the greater number of these fugitive accounts are permanently lost, yet the numerous contemporary "review articles" enable us to get a picture of the general attitude of the time.[16]

As we should expect, the philosophers of the seventeenth century were greatly impressed by the resemblance of the

[16] The reader is referred to Porta (1558), Bauhini (1616), Delrio (1633), Licetus (1634), Schurig (1732), and Haller (1757-66). *The Ephemerides Germanorum* or *Leopoldina* also contains numerous descriptions of these monsters. (See Decury I, Ann. 2, Obs. 58, 160, 250; Decury II, Ann. 4 Appendix p. 186, 193, Ann. 5, Obs. 153, Ann. 6, Obs. 41, etc.)



FRONTISPIECE OF
DE MONSTRORUM NATURA CAUSSIS

higher anthropoids to the human stock. It seemed reasonable on *a priori* grounds that apes and men could interbreed, and naturally accounts of such happenings were not lacking. Passages mentioning this hybridization have already been quoted from Ælian (p. 51), Buzurg ibn Shahriyar (p. 52) and Bartholini (p. 55). Caspar Bauhini in *De Hermaphroditis*, Oppenheim, 1614, discussed this matter as follows. From Bk. I, ch. 10, p. *m*111ff):

Ælian testifies that women copulate with dog-headed apes, a thing that Pindar seems to wonder at: adding that he had heard that these *cynocephali* had once loved virgins desperately, and, aroused by passion, had forced them using greater violence than those youths in the *Pannychidums* tale of Menander. He had heard likewise that the Indians do not bring red apes into the cities because, inflamed by passion, they may become violent with the female sex, and if ever they discover these apes, they pursue them with hate as if they were adulterous and kill them.

Fortunius Licetus in *De Monstrorum causis, natura et differentis*, Patavii, 1634, tells the story of an unfortunate woman. (From Bk. II, Ch. 68, p. 217):

They agree in this opinion which Castavenda reported in the Annals of Lusitania concerning sons born from a woman and an ape: That a woman because of a certain crime had been carried by ship to a desert island, and when she had been put out there, she was surrounded by a murmuring multitude of apes with which the place was crowded. One of the larger apes, to whom others yielded the ground, approached the woman and led her away with a gentle hand to a large cave. The ape together with his followers placed before her a supply of apples, nuts, and various roots, and invited her by a nod to eat. At last she was forced by the beast into dishonor, and this deed continued for many days so that she bore two children from the wild beast. And so, miserable (how much more desirable would have been death) she lived through some years until God, feeling pity, drove a Lusitanian ship there, and when the soldiers had gone up by chance to the watery upland hard by the cave, and

when the ape by good fortune was absent, the woman ran to the humans long unseen and falling at their feet begged that they snatch her away because of the deed and her very disastrous slavery. The soldiers pitied her in her trouble and agreed. She embarked with them on the ship. But behold, the ape coming upon them called back with confused gestures and noises to his wife (who was not his wife). When he saw the sails given to the winds, with a mad rush, he showed one of the children to the mother and threatened that unless she returned, he would cast it after the mother, nor did he do slowly that which he threatened. Then he ran back to the cave and with the same speed returning to the shore with the child, he pointed it out, threatened, and plunged it in the water. The child followed the mother until the waves overcame it as it swam. The whole affair is very well known by a Lusitanian witness and the woman was given over to be burned by King Ulyssixone but her life having been spared by the prayers of certain ones, he replaced death with perpetual imprisonment.

The great English philosopher, John Locke, referred briefly to women mating with baboons in his *Essay Concerning Human Understanding* published in 1690. The following paragraph on hybridization shows what a great English philosopher could achieve.

. . . for if history lye not, women have conceived by drills; and what real species, by that measure, such a production will be in nature, will be a new question: and we have reason to think this is not impossible, since mules and jumasts, the one from the mixture of an ass and a mare, the other from the mixture of a bull and a mare, are so frequent in the world. I once saw a creature that was the issue of a cat and a rat, and had the plain marks of both about it; wherein nature appeared to have followed the pattern of neither sort alone, but to have jumbled them together.

Antonio Zuccheli described the matter in more detail. From *Merckwurdige Missions und Reise Beschreibung nach Kongo in Ethiopien,* Frankfurt a. M, 1715 (pp. 147-148):

. . . and because they are all crowded together, it frequently happens that the negresses have to do with the great monkeys or apes, conceive by them and finally, after they have become pregnant, bring monsters into the world. A few years ago this very thing happened in this city of Loanda. Two black women of the same type became pregnant and when their time came bore two monkeys into the world, one of these fell to the lot of the Governor, and he took it with him to Lisbon on his return to Portugal; the other was given to our Padre at Loanda and lived several years in the hospital and finally died, and all of the people saw it and knew it and have verified the fact that its outward form was nearer to the human than to the monkey.

This brief survey of ancient and medieval beliefs concerning hybridization may well end with the contribution of John Ray. Ray preached a series of sermons on natural theology some time before 1660. In 1691 the material in these sermons was published under the title *The Wisdom of God Manifested in the Works of Creation.* The following quotation is taken from pages 295-297 of the eleventh edition, issued in 1743. In these remarkable paragraphs, Ray anticipated the pangenesis hypothesis of Darwin, described alternate or Mendelian inheritance of human hair color, and frankly gave up the problem of the mule's sterility as a mystery beyond human understanding:

Yet must it be confess'd that the Seed of Animals is admirably qualified to be fashion'd and form'd by the *Plastick Nature* onto an organical Body, containing the Principles or component Particles of all the several homogeneous Parts thereof; for indeed every part of the Body seems to club and contribute to the Seed,[17] else why

[17] The pangenesis hypothesis did not, of course, originate with Darwin. Its essential features were described not only by Ray (1691) but by Buffon (1748) in his *Histoire des Animaux* ch. 12, by Maupertius (1751) in the *Système de la Nature,* and by von Haller (1757-1766) in *Elementa Physiologie.* Von Haller stated, "The head contains germs of the tail and the tail germs of the head, so that when one is cut off the other furnishes a supply of germs, and these consequently receiving more nutriment are developed." Venette (1687) stated (p. 538), ". . . it is true, as I have proved elsewhere, that the seed is given life and that it comes from all parts of the bodies

should Parents that are born blind or deaf or that want a finger or any other Part, or have one superfluous, sometimes generate Children that have the same Defects or Imperfections; and yet (which is wonderful) nothing of the body or grosser Matter of the Seed comes near the first Principle of the *Fœtus*, or in some so much so as enters the Womb, but only some contagious Vapor or subtle *Effluviums* thereof, which seems to animate the *Gemma* or *Cictricula* of the Egg contain'd in the Female *Ovary* before it passes thro' the *Tubes* or *Cornua* into the *Uterus*. How far the Animalcules observ'd in the Seed of Males may contribute to generation, I leave to the more sagacious Philosophers to enquire, and shall here content myself without referring the Reader to the several Letters published by Mr. *Lewenhoek*.

But to what shall we attribute the *Fœtus* its likenesses to the Parents, or omitting them, to the precedent Progenitors; as I have observ'd some Parents that have been both black hair'd, to have generated most red hair'd Children, because their Ancestors Hair hath been of that Colour? Or why are Twins so often extremely alike? Where this is owing to the Efficient, or to the Matter?

Those *Effluvia* we spake of in the Male Seed, as subtile as they are, yet have they a great, if not the Greatest Stroke in Generation, as is clearly demonstrable in a Mule, which doth more resemble the Male Parent, that is, the Ass, than the Female, or Horse. But now, why such different *Species* should not only mingle together, but also generate an Animal, and yet that that hybridous Production should not again generate, and so a new Race be carry'd on, but Nature should stop here, and proceed no further, is to me a Mystery, and unaccountable.

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of the two sexes, as experience shows us. . . ." The idea that the different parts of the body contributed specific characteristics to the semen is very old. It was held by Hippocrates (c. 400 B.C.) and Democritos (c. 420-c. 370 B.C.). Hippocrates believed implicitly in the inheritance of acquired characters. In *Airs, Waters, Places*, §14, he stated, "For the seed comes from all parts of the body, healthy seed from healthy parts, diseased seed from diseased parts." Like statements are also to be found in Hippocrates' *Sacred Disease* and in his *Generation* (§3). Aristotle combatted this belief (*De generatione animalium*, Bk. I. ch. 17, 18) but it reappeared in *An animal sit id, quod in utero est*, a short treatise falsely assigned to Galen, and it was accepted by Paracelsus (*De generatione hominis*). The writer has recently traced the history of pangenesis in some detail (Zirkle 1935).

II

DEGENERATION AND THE DELAYED DISCOVERY OF PLANT HYBRIDS

I. THE MEANING OF "MALE," "FEMALE," "BASTARD," ETC.

A NUMBER of special precautions are necessary when we search old records for evidences of hybridization. The ancient and medieval writers were not only vague when they described the mating of unlike forms, but they also gave the word "sex" itself a number of peculiar meanings. They even assigned it to inanimate objects, and while this use of the term was often meant to be figurative and for the purposes of classification only, the figurative and literal uses were at times confused. It is possible that they were never completely separated. Precious stones were sometimes held to be male or female, and diamonds supposedly would multiply if the two sexes were only allowed free opportunity. The *Travels of John Mandeville*, composed about 1350, discloses the method.

> And the diamonds grow together, male and female. And they be nourished with the dew of heaven. And they engender commonly and bring forth small children, that multiply and grow all the year. I have oftimes assayed, that if a man keep them with a little of the rock and wet them with May-dew oft-sithes, they shall grow every year, and the small will wax great.

Even the Assyrians, who understood sex in the date palm, used the terms "male" and "female" in quite a different sense when applying them to other plants. According to Thompson (1924) a variety of cyperus was known as "male" probably because it was used to plait in charms for men. One species of mandrake was "male" another "female." Centuries later

the fruit of the male species was called "Devil's testicles" by the Arabs, a possible explanation of its male designation. *Liquidambar orientalis* was called "male" or "female" according to the shape of its gum. The larger of two kindred species was generally the male, the smaller the female. Even as late as the seventeenth century the wood of male trees was supposed to be harder than the wood of the females, although John Evelyn in 1680 recognized that this use of the term was figurative. From *Sylva* (p. 165):

> And in this work the *Ax* will tell you the difference of the *Sex;* the *Male* being so much harder and browner than the *Female:* But here (and whenever we speak thus of *Plants*) you are to understand the analogical, not proper distinction.

This analogical use of the term was quite the usual one, for more than fifty distinct species of plants were classified as male and female by Gerard (1633).

Another word apt to cause confusion in the interpretation of old records is "bastard." Gerard devoted eighteen whole chapters to various bastard plants and in addition described numerous bastards among the true species. When the term "bastard" was applied to a plant, however, it did not mean that the plant was a hybrid, but merely that it was unpopular. It was thus really an epithet and was frequently used to describe wild or native forms in contrast to the "true" or cultivated garden varieties. Consequently it designated species which had *not* been hybridized. A relic of this older passage still persists in the name "bastard toad-flax." Praeger (1932) pointed out an interesting passage in Shakespeare's *A Winter's Tale,* in which the epithet "bastard" is applied to the gillyflowers:

> *Perdita*
>
> . . . the fairest flowers o' the season
> Are our carnation, and streak'd gillyvors
> Which some call nature's bastards: of that kind

Our rustic garden's barren; and I care not
To get slips of them.

Polixenes

Wherefore, gentle maiden,
Do you neglect them?

Perdita

For I have heard it said,
There is an art which in their piedness shares
With great creating nature.

Polixenes

Say, there be;
Yet nature is made better by no mean
But nature makes that mean; so, o'er that art,
Which you say adds to nature, is an art
That nature makes. You see, sweet maid, we marry
A gentler scion to the wildest stock;
And make conceive a bark of baser kind
By bud of nobler race: This is an art
Which does mend nature,—change it rather; but
The art itself is nature.

Perdita

So it is.

Polixenes

Then make your garden rich in gillyvors,
And do not call them bastards.

It appears from the above that bastard plants were considered artificial and to some extent unnatural, yet the last line shows that the word was essentially an epithet. It is necessary that we understand clearly that this term had no connotations of hybridity when it was used by the sixteenth- and seventeenth-century naturalists. Otherwise we should be apt to misunderstand the records, particularly those wherein a

heterozygous plant happened to be labeled a bastard. Perhaps the best example of such an accidental use of the word is to be found in a short passage in Sharrock (1660). This could easily be mistaken for an authentic record of plant hybridization, for it is a very real trap for the unsuspecting biologist. Thus:

> The two lesser Spanish bastard Daffodills, the leaves of which are of a whitish green color, one a little broader than the other, and the flowers pure white, bending down their heads, that they almost touch the Stalk again, give Seed from which springs much varietye, few or none keeping either colour of height with their mother plant.

Sharrock, however, was merely listing another instance of degeneration which is clearly shown by the context. (See page 75.) More than a hundred years passed before the term "bastard" acquired its modern meaning, for its earliest unambiguous application to a hybrid plant which we have yet found, occurred in a letter written in 1775. (See page 188.) Even the word "hybrid" is not entirely unambiguous, for Linnæus used it to designate a flower which contained both pistils and stamens.

2. DEGENERATION IN THE VEGETABLE REALM

Although gardeners and agriculturists on the whole were ignorant of the function of pollen, its use was well understood in the learned world. Long before Grew made his famous address to the Royal Society (1676), many excellent descriptions of pollination had been published (John Leo 1526, Prosper Alpino 1592, George Sandes 1610, Chas. de l'Ecluse 1611, Fabri 1620, Larembergii 1654, etc.). Moreover the variability of garden plants was recognized, and combinations of diverse characteristics were known to occur. It seems remarkable, therefore, that spontaneous hybridization was not recognized earlier. The delay may have been caused by the widespread belief in degeneration, or the spontaneous trans-

mutation of species. Cultivation was observed to alter wild plants, and it seemed to the philosophers but a logical exterpolation to assume that under certain conditions one species would degenerate into another. This belief was recorded by Theophrastos as early as the third century B.C., and he was followed in this by most of the classical authors who wrote on agriculture. It is obvious, for example, how a belief could arise in the degeneration of wheat into oats, or rye into barley, when the small grains became mixed through a careless selection of seeds. Thus, hybridization remained an unneeded hypothesis. In the *Causis Plantarum* (Bk. II, ch. 13), Theophrastos describes some of these changes due to cultivation:

It is evident that the changes in fruits when they are transplanted to new regions follow the variations of the soil and of the sky, for from these two things and through them nourishment is supplied for all vegetation. For much food is too powerful for assimilation, if indeed the likeness of these fruits to the animal kingdom is similarly reflected. Not only do we see seeds, plants and trees change, but even animals, and the latter in a particular fashion inasmuch as they take on forms similar to the nature of their localities, while in plants this is not equally evident. But there is also some adaptation in the case of plants, principally noticeable in their color, size and shape. The seeds are changed mainly in color; they turn from black to white and from white to black. So also the fruit with its juice, but the change of color in fruits is either not evident or is not accomplished in the same way, unless indeed the whole tree becomes likewise changed, so that the black fruit becomes white, a mutation which sometimes takes place in the case of those which have grown from seed. Since this attribute is common to plants and animals, however, we must seek a common cause. For plant life and animal life agree in this, that they are not changed immediately, but only eventually—at the third generation. For all of them change and are altered gradually. But the fashion of trees is contrariwise, for they are not at all strong at first, especially when they are raised from seed. The change in the genus of trees is especially singular and

worthy of wonderment as when the fruit improves, as we have recorded in the case of the pomegranate in Egypt and even more so in Cilicia, and of the pleasant odor of the myrtle in Egypt. For we observe that very often changes are made for the worse everywhere, and we do not wonder at them, but at the same time it is evident that what happens in seeds, though they are changed for the better, is a similar process. For the sole difference is that trees always remain in the same place after they have been planted, but seeds enter upon new conditions at every fresh sowing. For the change is the same in both, for something which holds nature vanquished, is removed in the same way from each of them. For the same thing happens in the animal kingdom when animals change color from black to white, and their harsh coats become smoothe, and they undergo other changes of the same sort. When you observe that manifest causes are the authors of the change, such causes as water in some cases, in others food and air, you may rightly suppose that something similar happens in the case of both plants and animals to accomplish the same or similar results. In the case of individuals, however, the better or perhaps the only method seems to be to call in the aid of experience and to explore the nature of the locality where they grow.

Virgil in the *Georgics* described the transmutation of grains, and Pliny states:

The first and principal defect observed in bread-corn, and wheat especially, is when it doth degenerate and turn into Otes; and not only it but Barley also doth the like.

The following quotation from *De Plantis* of Nicolaus Damascenus, which is possibly Aristotle once removed, shows that the transmutation of species was thought to differ only in degree from the changes induced by cultivation. The fact that this work contains statements contradictory to some in the well-authenticated works of Aristotle is no proof that he is not the author, as the early philosophers did not overburden themselves with consistency.

Likewise, certain of the plants are changed to another species; for example, the nut, after it has reached a certain age. It is said

also that calamentum [the fragrant herb sisymbrium?] is changed into mint. The aromatic plant basil, cut off and transplanted beside the Green Sea [i. e., the Persian Gulf; acc. to note, mistranslated from the Arabic for "during the extreme heat of the summer"], will perhaps become thyme. Wheat also and flax are changed into darnel. Likewise, the poisonous *belenum* [Persea] native to Persia undergoes transformation, and has become edible on being transplanted to Egypt and Syria. The unfruitfulness of almond and pomegranate trees also can be altered by a special culture. Pomegranates are improved by fertilizing them with pig dung and by supplying them with cold fresh water. Also almond trees that have nails driven into them give out gum over a long period of time. Thus by artificial culture many wild plants are becoming domesticated.

Early descriptions of other cultivated plants indicate that they also had resulted from certain fortunate crosses. The degeneration of olive seedlings was so well known that St. Augustine (419-420 A.D.) used it as an argument for the necessity of baptism. From *Marriage and Concupiscence* (Book I, chapter 21):

It is, no doubt, very wonderful that what has been remitted in the parent should still be contracted in the offspring; but nevertheless such is the case. That this mysterious verity, which unbelievers neither see nor believe, might get some palpable evidence in its support, God in his providence has secured in the example of certain trees. For why should we not suppose that for this very purpose the wild olive springs from the olive? Is it not indeed credible that, in a thing which has been created for the use of mankind, the Creator provided and appointed what should afford an instructive example, applicable to the human race? Is it a wonderful thing, then, how those who themselves have been delivered by grace from the bondage of sin, should still beget those who are tied and bound by the self-same chain, and who require the same process of loosening? Yes, and we admit the wonderful fact. But that the embryo of wild olive trees should latently exist in the germs of true olives, who would deem credible, if it were not proved true by experiment and ob-

servation? In the same manner, therefore, as a wild olive grows out of the seed of the wild olive, and from the seed of the true olive springs also nothing but a wild olive, notwithstanding the very great difference there is between the wild olive and the olive; so what is born in the flesh, either of a sinner or of a just man, is in both instances a sinner, notwithstanding the vast distinction which exists between the sinner and the righteous man.[1]

It would be tedious to list all of the records of degeneration which appeared in the thousand years following St. Augustine. During this time the savants believed in the spontaneous fluctuation of species as firmly as they did in the equivocal generation of life. St. Augustine himself is credited with holding evolutionary views, which is not remarkable, for the belief in the constancy of species, as a scientific tenet, was still far in the future.

Of special interest to us is the work of Peter of Crescentiis who wrote *Opus ruralium commodorum* in 1305. Here the fluctuation of species is described in great detail in Book II, chapters 8, 9, and 10.

During the sixteenth and seventeenth centuries the segregation of different types from a hybrid parent was observed by a number of scholars, whose writings show that they did not suspect the true cause of the variability.

Levinus Lemnius published *Occulta Naturae Miracula*, Antwerp, 1561. Chapter XVII of Book I, entitled *Herbas*

[1] This same idea was repeated by St. Augustine in chapter 37:

. . . That, however, which in the case of a regenerate parent, as in the seed of the pure olive, is covered without any guilt, which has been remitted, is still no doubt retained in the case of his offspring, which is yet unregenerate, as in the wild olive, with all its guilt, until then also it be remitted by the self-same grace. When Adam sinned, he was changed from that pure olive, which had no such corrupt seed whence should spring the bitter issue of the wild olive, into a wild olive tree; and, inasmuch as his sin was so great, that by it his nature became commensurately changed for the worse, he converted the entire race of man into a wild olive stock. The effect of this change we see illustrated, as has been said above, in the instance of these very trees. Whenever God's grace converts a sapling into a good olive, so that the fault of the first birth (that original sin which had been derived and contracted from the concupiscence of the flesh) is remitted, covered, and not imputed, there is still inherent in it that nature from which is born a wild olive, unless it, too, by the same grace, is by the second birth changed into a good olive.

Mutationibus, contains a four-thousand-word discussion of the alteration of species and varieties, which according to the author, were caused mainly by the methods of cultivation. The following quotation, which describes what are probably the effects of bud mutations, is from page 92 of the 1564 edition:

. . . Thus "gariophyllaea" [Dianthus?] bears white, red, and variegated flowers, and some with long stamens, all on one stalk because of either the fertility of the soil or of exceptional zeal in their cultivation. Sometimes their color varies from violet or purple to dark or light blue. Similar specimens have the advantage of many stems and leaves less crenate or serate; and "acanacra," that is, those which bristle with spines, are tamed by the nature of the location and of a mere sloping habitation and become almost spineless. From this I report what daily experience shows, that arbutus plants not only change their species, if they get a suitable location and atmosphere, but also grow better and more fruitful; they produce healthy plants, when just previously they might have produced lethal ones. Galen relates this about a Persian plant, which, according to Pliny, was brought over into Egypt.

Many other sixteenth- and seventeenth-century naturalists cited instances of this degeneration in plants. Even Charles de l'Ecluse (Carolus Clusius) described the segregation of genetic factors in hybrid tulips and peonies as mere degeneration, although he was well acquainted with the sexuality of the flowering plants. In *Rariorum aliquot stirpum per Hispanias observatarum,* Antwerp, 1576, he wrote of tulips, page 513:

V. The color combinations are so different that it is difficult to describe in words all of their variations. For when, finally, any early flowering tulips germinate from scattered seed buried in the earth, very few of them retain completely the color of the mother plants, but transform their flowers into different colors, although, for the most part, they degenerate into a muddy yellow. On the other hand,

some may be part white, part purple, others part red and part yellow and gold. Still others may be seen with colors mixed of yellow, orange, white, purple, and even red.

The description of peonies by l'Ecluse, in *Rariorum plantarum historia*, Antwerp, 1601, also shows clearly the segregation of different types from a hybrid ancestor. From page 279:

The seed of these in the year 1588 produced plants some of which resemble the mother in leaves, two in fact have leaves much more divided and with the segments further apart. These gave flowers three years afterward for the second time similar to the stock but with short and thick pods.

From page 281:

From a fertile flower filled with seed were born for me plants clearly resembling the mother in stem, leaves, and root. One of these plants in the third year produced a flower colored like that of the mother—but with a simple series of six petals. Another bore a flower like those of the first Byzantine, that is, having a simple series of eight petals. A third bore a complete flower, the same color as the mother, but somewhat larger, and in other years it bore cornicula or nuts some of which were pregnant with seed.

The degeneration of tulips was also noted by John Gerard and described by him in *The Herball, or General Historie of Plants*, London, 1597. Attempts were even made to investigate the inheritance of flower color, but without success. Gerard's account of this work should make every geneticist feel a very real sympathy for "my loving freind Master James Gerret." From Bk. I, p. 116-117:

. . . Of this there be two chiefe and generall kindes, *videl Praecox and Serotina*, the one doth beare his flowers timely, the other later: to these two, we will adde a third sort called *Media*, flowering between both the others. And from these three sorts, as from their heads, all other kinds do proceede, which are almost infinite in num-

ber. Notwithstanding my loving freind Master *James Garret*, a curious searcher of Simples, and learned Apothecarie in London, hath undertaken to finde out if it were possible, the infinite sorts by diligent sowing of their seedes, and by planting those of his owne propagation, and by others received from his friends beyond the seas, for the space of twentie yeeres, not being yet able to attaine to the end of his travaile, for that each new yeere bringeth foorth new plants of sundrie colours not before seene: all which to describe particularlie, were to roule *Sisphus* stone, or number the sandes: so that it shall suffice to speak & describe a few, referring the rest to som that meane to write of *Tulipa* a particular volume.

In the second edition of Gerard's *Herball*, Thomas Johnson quoted the classical records of degeneration and added an observation of his own, viz., the occurrence of grains of oats in an ear of wheat. An identical observation was made a hundred years later (letter of Peter Collinson to Sir Hans Sloane), and in this latter instance the cause assigned was hybridization. From Gerard's *Herball* (Ed. of 1633):

I think it a very fit thing to adde in this place a rare observation of the transmutation of one species into another, in plants; which though it have beene observed of ancient times, as by Theophrastus, *de caus, plant*, lib. 3, cap. 6, whereas amongst others hee mentioneth the change of Spelt into oates: and by Virgill in these verses;
Grandia saepe quibus mandavimus Hordea sulcis,
Infœlix Lolium steriles dominatur avenae.
That is—
In furrows where great Barley we did sow,
Nothing but Darnel and poore Oats do grow;
Yet none that I have read have observed, that two severall graines, perfect in each respect, did grow at any time in one eare; the which I saw this yeare, 1632, in an eare of White Wheat, which was found by my very good Friend Master John Goodyer, a man second to none in his industrie and searching of plants, nor in his judgement or knowledge of them. This eare of wheat was as large and faire as most are, and about the middle thereof grew there of foure perfect

Oats in all respects: which being hard to be found, I held very worthy of setting downe, for some reasons not to be insisted upon in this place.[2]

Johnson also noted that certain horticultural varieties of marigolds did not breed true from seed. The aberrant forms, however, were looked upon as sports; nature simply liked to play. From page 740:

7. This fruitfull or much bearing Marigold is likewise called of the vulgar sort of women Jacke-an-apes on horseback: it hath leaves, stalkes, and roots like the common sort of Marigold, differing in the shape of his flowers, for this plant doth bring forth at the top of the stalke one floure like of the other Marigold; from the which start forth sundry other small floures, yellow likewise, and of the same fashion as the first, which if I be not deceived commeth to passe *per accidens*, or by chance, as Nature oftentimes liketh to play with other floures, or as children are borne with two thumbs on one hand, and such like, which living to be men, do get children like unto others: even so is the seed of this Marigold, which if it be sowen, it brings forth not one floure in a thousand like the plant from which it was taken.

8. The other fruitful Marigold is doubtlesse a degenerate kinde, coming by chance from the seed of the double Marigold, where as for the most part the other commeth of the seed of the single floures, wherein consisteth the difference.

The same year (1633) in which this second edition of

[2] This mixture of two grains upon a single ear was reported several times during the seventeenth and eighteenth centuries. Worm described such an ear in 1655 (see page 73) and Hauser noted grains of oats on an ear of speltz (?) in 1711. From his *Theses Botanico-anatomical* (Thesis No. 25): "Several years previously I had been able to observe, through a curious spectacle of nature, a very suitable ear of spelts, which included near its base a grain of oats. This monstrocity I gladly observed. . . . After the grains of spelts were planted and watered the embryos started to germinate but the rest of the seeds rotted from too much moisture. The grain of oats, sown adjacent to the rotting grains of spelts was also partly spoiled by the moisture . . . because the embryos of spelts were stronger than that of the oats, more grains of spelts were produced than oats." Peter Collinson sent a specimen of such an ear to Sir Hans Sloane (see page 161), and in 1765 Nonne published a short paper entitled, *Quaedam de plantis nothis, occasione spicae Tritici, cui Avenae fatuae aliquot semina innata erant.*

Gerard appeared, Giov. Battiste Ferrario published his *Florum Cultura*. He described Mendelian segregation very clearly, yet, in keeping with the fashion of his time, he merely cited his findings as evidence of the spontaneous degeneration of horticultural varieties. From page 347:

One can produce many varieties from the seed of a white carnation. It is advantageous to sow speckled types among varieties with strange markings in order to produce a degenerate descendant, beautiful and mottled with a rich yellow color, and at times even an unblemished flower.

Ole Worm in *Museum Wormianum seu historia rerum rariorum*, Lugduni Batavorum, 1655, described an ear of barley which contained grains of rye:

Barley, which I called *Hermaphroditicum*, because it contains both barley and rye in a single ear. A man, Reverend D. Michael Butrup, Most Vigilant Pastor and President of the Parish of Greffne and Kildebreond, showed me such an ear; and he stumbled by chance upon this unique ear in his own field among the left-over crops. The ear is small, not exceeding a thumb's length and appearing at first sight to be barley. There are four uniform rows in each of which are five grains. The rows are so placed that one of barley may alternate with one of rye. Moreover these grains are placed in glumes in such a manner that the barley is furnished with long, strong, and sharp beards: the rye indeed is defrauded of these. Indeed certain sterile glumes intervene, destitute of grains. I did not search out such a union of unlike grains in a single ear, different from others, and therefore I consider that this certainly must not be overlooked.

Five years after Worm issued his catalogue, Robert Sharrock published *The History of the Propagation & Improvement of Vegetables by the Concurrence of Art and Nature*, Oxford, 1660. This work contained perhaps the best of all descriptions of degeneration in the plant kingdom. Sharrock was very skeptical as to the reported transmutation of wheat into oats and all such changes of species, but he had himself seen

Mendelian segregation in a number of the more commonly cultivated flowers. Moreover, the variable progeny which could be raised from the seed of a single plant convinced him that degeneration was a very real phenomena. The following quotations, which are taken from the first edition of this work, contain a number of obviously typographical errors. From Chapter I, g. 5, p. 25:

No. 5. *Of variety of kindes, different in colour, taste, smell, and other sensible qualities, proceeding from some seeds, and what plants they are that bring seeds yield—such variety.*

In Carnations you have seeds that give admirable Variety from the Orange-tawny Carnation and all his strip't kinds that are double and keepe their tawny in them in any measure. The white, Tawny and Carnations darkly spotted, *Ferrarius* commends for producing variety of colours and stripes. Kernells of divers Apples and Peares bring variety of Kinds, different in taste, smell, colour, and hardnesse, and are as often promoted to better, as the degenerate to worst, as I am very credibly informed, by persons that professe themselves to have seen The Experience. The kernells of the Burgundy Pear has brought a noble alteration and produceth a pear farre beyond that excellent kind: Peaches and Malecotones doe ordinarily the like, so that by seed is thought to be their best propagation.

Our Gardiners in choosing the seed of stock-Gylliflowers to make them bring double stocks, take their seed from such tops as bring fine leaves in their flower, especially if it be one strip't; but Mr. *P.* sayes those that bear double seeds, cannot be distinguished from the other, and I have reason to believe him, for such as chuse their seed this way, doe not find that it answers their expectation.

For Tulips that are early, or Praecoces, purple says Mr. *Parkinson*, I have found to be the best, next therto is the purple with the white edges, and so likewise the red, with yellow edges; but each of them will bring most of their own colours. For the Media's, take those colours that are light, rather white than yellow, and purple, then red, yea white, not yellow, purple, not red: but these again to be spotted is the best, and the more the better; but withall or aboveall, in these respects the bottome of the flower (which in the precox

Tulipa you cannot, because you shall find no other ground in them but yellow) for if the flower be white or whitish, spotted, or edged and straked, and the bottome blew or purple (which is found in the Holias, and in the Cloath of Silver, this is beyond all other the most excellent, and out of question the choisest of our hundred, to beget the greatest and most pleasant variety, and raritie, and so in degree the meaner in beauty you sow, the lesser shall your pleasure in varieties be: Bestow not your time in sowing red or yellow Tulipa-seed, or the diverse mixtures of them, the[y] will (as I have found by experience) seldome be worth your paines. The Serolina being not beautifull, brings forth no speciall varietye: *Ferrarius* lib. 3, chap. 7. commends the Serolina for seed, (but I find he makes but two sorts; Praecoces and Serolin's) and among them the white, with the black purple, or blew bottomes or Scarlet with skycoloured bottome inclining to purple; for both them will (sayes He) bring Tulips mark't with varietye and handsomenesse: but Tulips without a blackish bottome are noe good breeders of various coloured flowers.

The two lesser Spanish bastard Daffodils, the leaves of which are of a whitish green colour, on a little broader than the other, and the flowers pure white, bending down their heads, that they almost touch the Stalk again, give Seed from which springs much varietye, few or none keeping either colour or height with their mother plant. The seeds of divers Sowbreads, by name the Roman Sowbred with round leaves, the Autumnall Ivy leaved Sowbread, some flowers de-lis, and many sorts of Bears-eares doe the like in producing admirable variety.

As for Anemones, take't from Mr. *P.* and our common dayly experience that there is not so great variety of double flowers raised from the seeds of thinne leave'd Anemones as from the broad leaved ones. Of the datifolias, the double Orange-tawny seed being sowen, yeildeth pretty varietyes, but the purples, or reds, or crimsons, yeild small varietyes, but such as draw nearest to their originall, although some be a little deeper or lighter than others: but the light colours are they that are chief for choice, as white, ash-colours, blush or Carnation, light Orange, Simple, or party-coloured, single (or double if they bear seed) which must be carefully gathered, and that not before it be fully ripe, which you shall know by the head, for when the seed with the woollinesse beginneth a little to rise out of itself at

the lower end, then must it be quickly gathered, lest the wind carry it all away, after it is thus carefully gather's it must be layd to dry for a week or more, which then being gently rubbed with a little dry sand, or earth will cause the seed to be better separated, although not thoroughly, from the wooliness or downe that compasseth it. In the seed of the Mervayle-of-the-world, take notice, that if you would have variable flowers, you must chuse out such flowers as be variable while they blow, that you may have their seed! for in this plant, if the flower be of a single colour, the seed will likely bring the same.

In No. 6, "*Some other relations touching transmutation and the possibility of the change of one Species into another, examined in particulars of the Vegetable, Animal and Mineral Kingdoms,*" Sharrock explained correctly the causes of the supposed changes in species of small grains. He could not entirely escape the spirit of his time, however, and he included, almost apologetically, the following. From pp. 29-30:

It is indeed growen to be a great question, whether the transmutation of a species be possible either in the vegetable, Animal, or Mineralle kingdome. For the possibility of it in the vegetable: I have heard Mr. *Bobart* and his *Son* often report it, and proffer to make oath that the Crocus and Gladiolus, as likewise the Leucoium, and Hyacinths by a long standing without replanting have in his garden changed from one kind to the other: and for satisfaction about the curiosity in the presence of Mr. *Boyle* I tooke up some bulbs of the very numericall roots whereof the relation was made, though the alteration was perfected before, where we saw the diverse bulbs growing as it were on the same stoole, close together, but no bulb half of the one kind, and the other half of the other: But the change-time being past it was reason we should believe the report of good artists in matters of their own faculty.

Mr. *Wrench* a skilfull, and industrious gardiner for fruit and kitching-plants told me that the last year there was a change betwext the kinds of the Cole-flower, and the cabbage. Others I know

who as from their experience most confidently affirme that they have prime-roses of the milk white colour, the root whereof before in another ground bare Oxelips: and it is usually believed that single flowers may be changed into double by frequent transplantations, made into better grounds. I know that those who have had the wood Anemonies, and Colchiums double, who affirme that they took them into their garden wild, and single, and that that change was made by the soyle, and culture of the place.

This spontaneous hybridization in the cabbage family (*Brassica*) was to worry the philosophers for nearly a hundred years.

In 1680 Robert Morison published *Plantarum Historiae universalis Oxoniensis* and incidentally he described many instances of the degeneration of plants. He noted particularly the behavior of several varieties of *Brassica* and interpreted the instability of this genus as a very delicate reaction to environmental influence, especially the influence of different types of soil. He stated that "All these species of *Brassica* sprout in a remarkable manner and at alternate plantings are transmuted into each other," a rather interesting observation of dominance and Mendelian segregation. Wahlbom, in 1746, assigned this fluctuation of species to cross-pollination (see page 163), and Philip Miller, from a different set of observations made in 1721, came to the same conclusions (see page 126). The following quotation is from the 1715, or posthumous edition of Morison's works (Vol. I, pp. 208-209):

We have observed this Brassica persevering in the chalk cliffs in the vicinity of Dover in the year 1657 and afterwards in the year 1660. It continued for many years at London in the garden of Edward Morgan and in the public garden of the University and it brought forth its seeds in abundance every year. We called it the Maritime Cabbage (*Brassica Maritima*) because we came upon it in the aforesaid location [i.e., by Dover]; or else we called it the *arborea procerior*, because of its height and its branchings and be-

cause of the great number of small branches which it bore, all of which indicate that it differs specifically from the rest of the *Silvestri*, especially from the so-called Cramlee [cabbage], of the species *Silvester Dioscores* or *Silvester Dodanaeus*. All these species of Brassica sprout in a remarkable manner and at alternate plantings are transmuted into each other; for in a field which abounds in salt and has been well fertilized, red and white headed cabbages are procreated from the *Brassica sativa aperta*, or the vulgar white and red, and from the seeds of those same plants, when planted in a field which is full of sand and gravel, and barren, plants are grown which resume their former status. They become ordinary unheaded cabbage in wooded gardens which are not manured, to the extent that we have seen an open Cabbage develop from the seeds of white and red headed Cabbage and grow to a height of ten cubits. Likewise the seeds of the *Brassica Tophosa* were sent from Italy to that most Reverend Father in Christ, Henry Compton, Bishop of London; they produced a *Brassica Tophosa* in his garden at Oxford and in the public Botanical garden of the University, but its seed sown for a second time degenerated into the *Vulgaris Aperta Lavis*. The same thing must be said of the *Brassica florida* Botrys, seed of which was recently sent to us from India; it produced *Brassica Floridae*, but their seed, collected and sown in England, degenerate into the *Brassica longifolia et aperta*, a fact which experience has made known to all, but to no man more so than to Richard Baal, the gardener at Bramford, who collected in his own garden a large number of seeds from the *Brassica florida*, which he sold to gardeners, very many of whom lived in suburban districts of London, vulgarly known as "Neat Houses," and these men committed those same seeds with the greatest care and industry to earth well fertilized by many years, but these seeds produced for them the large *Brassica longifolia aperta!* For this reason the aforementioned gardeners, noting that they had lost their work and their toil; that is, that they had expended their industry, care, labor, at great expense and without return, nay, with the greatest detriment and expenditure of time and money, started a lawsuit against the aforesaid Baal in the Court at Westminster and the decision of the Judges sitting there not only condemned him

to restore to the men the money which he had received from them, but in addition that same Baal was fined that he might recompense the aforesaid gardeners for the waste of their time, their expense and the use of their ground.

The seeds of the *Brassica Labanda*, summer and winter varieties, sent to us from Italy thrives excellently in England, but the seeds of that same variety collected here degenerate into the *Brassica aperta*. The *Brassica asparagodes* occasionally send forth curly little leaves in abundance from the ribs and veins of the leaves, but sometimes they send forth none but degenerate into the *Vulgaris crispa*. Thus any veteran gardener can easily observe the permutations and degenerations of *Brassicae* from one species to another.

The above passage has had a most interesting history. In 1686 John Ray copied it almost word for word and included it in the chapter on degeneration in his *Historia Plantarum*. The part of Ray's copy which described the misadventures of the unfortunate Baal was in turn quoted by Johann Wahlbom, one of Linnæus' students (1746). It was incorporated in Wahlbom's dissertation in the paragraph following his account of the hybridization of tulips. Sachs, in his *Geschichte der Botanik* (1875), credited Wahlbom's paper to Linnæus. The following quotation from Sachs's history shows how supercilious and inaccurate he was:

> Soon after allusion is made to the artifices used by gardeners to obtain hybrid tulips and cabbages, but the matter is treated rather as agreeable trifling.

3. INTIMATIONS OF PLANT HYBRIDS

Undoubtedly many of the changes which occurred so frequently in cultivated vegetables were really caused by cross pollination of nearly related species. Actual evidence of widespread hybridity in domestic plants is attested by the fact that fruit trees and other horticulture varieties do not breed true from seed, but have to be reproduced vegetatively. The horti-

cultural methods which insured the hybrid natures of dates and figs have already been described (Chapter I).

It is almost certain that this hybridization was entirely incidental and that the Babylonians and Assyrians who were responsible for it appreciated neither the opportunities nor risks of cross pollination, although there is a possibility that the Hebrews had some vague conception of the effects of contamination with foreign pollen. They recognized the function of pollen, at least in the date palm, for they cultivated this tree in the vicinity of Jericho for over a thousand years. Of course we must be careful not to read too much into the records, but some of the prohibitions in the following verses would have more meaning if plant hybridization had been recognized as a possibility. From *Lev.* 19:19:

> Ye shall keep my statutes. Thou shalt not let thy cattle gender with a diverse kind; thou shalt not sow thy field with mingled seed; neither shall a garment mingled of linen and woolen come upon thee.

From *Deut.* 22:9:

> Thou shalt not sow thy vineyard with diverse seeds; lest the fruit of thy seed which thou hast sown, and the fruit of thy vineyard be defiled.[3]

Possibly these commands had no biological significance. One somewhat obscure passage in the work of an Arabian scientist, however, may indicate that he at least recognized the influence of the pollen on the character of the progeny. We may even have to recognize Ibn-Al'awwam (1150?-1200?) as the first plant hybridizer. His work was translated into Spanish by J. A. Banqueri and published as *Libro de Agricultura*,

[3] Flavius Josephus, in *Antiquities of the Jews* (Bk. IV, ch. 8), gave the reasons for this prohibition: "The seeds are also to be pure and without mixture, and not to be compounded of two or three sorts, since nature does not rejoice in the union of things that are not in their own nature alike; nor are you to permit the beasts of different kinds to gender together, for there is reason to fear that this unnatural abuse may extend from beasts of different kinds to men, though it takes its first rise from evil practices about much smaller things."

Madrid, 1810. The following quotation is taken from Vol. I, p. 349:

> The palm fertilized by the male plant in blossom time produces delicate and succulent dates. I have fertilized a wild palm in "El Alxarafe" at the time its blossoms were unfolding by sprinkling on it the pulverized blossoms of the male plant, and there sprouted in that vicinity dates of equal quality.

Another Arabian scientist, Abd-al-Latif (1162-1231), described the mixing of various citrus fruits. He noted that oranges and lemons, when grown near each other, combined and produced new varieties. From his *Description of Egypt*, Bk. II (Wahl's translation p. 89): "When one plants these species which resemble one another near together, one can obtain from them innumerable varieties." This passage does not necessarily indicate that Abd-al-Latif understood pollination and plant hybridization. If we interpret it in the light of his description of the origin of the banana, its meaning becomes quite vague. At a time when both the Christians and the Mahometans located the Garden of Eden in no very distant country, and when it was generally believed that the Garden had contained all of the really good plants, it is obvious that a recently introduced species from southeastern Asia, such as the banana, would cause some speculation. Its place of origin was naturally soon forgotten, and, as it was not mentioned in the old and revered documents, it must have come suddenly into existence. Abd-al-Latif's story of its creation shows that the writer believed a new plant could emerge from a union of two unlike forms without involving the sexual elements of the flowers. The following quotation is taken from the French translation of Silvestre de Sacy, *Relation de l'Egypt*, etc., Paris, 1810, page 26:

> It is affirmed that the banana tree came originally from a mixture of the Egyptian water-lily and the seed of the date; in order to produce this composite vegetable it is necessary to force a date-seed

into the interior of the corm (?) of the water-lily and to plant it in this manner.[4]

Peter of Crescentius (1305) should also be placed among the medieval writers who considered the possibility of blending two different species in order to form a third. Although he knew of plant sexuality in the date palm, his method of combining the different types of plants was but a variation of the ancient technique of grafting. From *Opus ruralium commodorum*, Bk. II, ch. 9:

Besides this there is the fact that some trees are called male and some female. And it is known that the male tree buds forth before the female because of the heat that moves there with more force, and the leaves are straighter and smaller because of the dryness of the male, which also is the case in many other plants and especially in the palm-trees, where the spathe and the pollen of the male, placed above the branches of the female, both aids in generation and in the maturation of fruits of the female. The same happens when a male tree is planted near a female tree, so that the scent of the male may be carried to the female by the wind. Likewise if pomegranate trees are planted near the olive trees, so that the vapor may gradually cross over to the female olive trees, it helps much. On the other hand, when some trees unite with others, they hinder fructification and generation, just as the cornelian-tree harms the vine, and as the walnut-tree is harmful to most other plants because of its mortal bitterness.

From Bk. II, ch. 8:

It has also been proven that when the branches are inserted into

[4] Salvatore Cusa in *Il libro interno alle palme*, p. 338-339, describes this method of hybridization in more detail:

Although the oriental people, fond of marvelous products, had always been carried away by the idea of grafts to the point of having recourse to operations most strange and also immoral (the reason why, according to Maimonide, Moses had prohibited their use to the Hebrews), still, nevertheless, in the palm, because of its slight affinity with other plants, grafts were little used. One, however, was used, of the palm on the colocasia (water-lily) from which they believed sprung a fine banana. For this purpose, they directed, you shall make an incision with a gold knife in the foot of the colocasia and within this you shall put a fruit-stone of the female date, which is shorter and rounder than the male, you shall bind it completely and cover it with sticky clay, mixed with a few hairs covered with plant soil. Having done this grafting in January you will be able to gather fruit of the banana in July or August.

the trunk of the peach-tree or of the dog-rose, the nature of the two trees change, and the fruits become larger and better, not like the other fruits. And this same thing happens also in animals in the mixture of similar seeds in nature, as in asses and mares, from which mules are produced. Therefore, the peach-tree is not very different or dissimilar from the bramble, or the dog-rose. . . .

Inasmuch as the valid internal evidence of hybridity was universally explained by the hypothesis of degeneration, the first speculations concerned with plant hybridization were not inspired by a study of the plants themselves, but by the recognition of animal hybrids. Thus Francis Bacon was led to contemplate the possibility of plant hybrids. He knew of the sexual reproduction of the date palm, but his account of it is very fanciful and inaccurate when compared with the descriptions given by his contemporaries, Alpino and Sandys. As far as Bacon was concerned, sexual reproduction in plants was merely a longitudinal fusion of twigs. He was interested, however, as Cook (1932) has pointed out, in the possibility of securing new forms of plants through hybridization. The following extract is taken from *Sylva Sylvarum* (1626):

Experiments in Consort Touching Compound Fruits and Flowers

We see that in living creatures, that have male and female, there is copulation of several kinds; and so compound creatures, as the mule, that is generated betwixt the horse and the ass, and some other compounds which we call monsters, though more rare; and it is held that the proverb, *Africa semper aliquid monstri parit*, cometh, for that the fountains of the waters there being rare, diverse sorts of beasts come from several parts to drink, and being so refreshed, fall to couple, and many times with many kinds. The compounding or mixture of kinds in plants is not found out; which, nevertheless, if it be possible, is more at command than that of living creatures, for that their lust requireth a voluntary motion; wherefor, it were one of the most noble experiments touching plants to find it out; for so you may have great variety of new fruits and flowers yet unknown. Grafting doth it not, that mendeth the fruit or doubleth the flowers,

etc., but it hath not the power to make a new kind. For the scion ever over-ruleth the stock.

It hath been set down by one of the ancients, that if you take two twigs of several fruit-trees, and flat them on the sides, and then bind them close together and set them in the ground, they will come up in one stock; but yet they will put forth their several fruits without any commixture in the fruit. Wherein note by the way, that unity of continuance is easier to procure than unity of species. It is reported, also, that vines of red and white grapes being set in the ground, and the upper parts being flatted and bound close together, will put forth grapes of several colours upon the same branch; and grape stones of several colours within the same grape: but the more after a year or two, the unity, as it seemeth, growing more perfect. And this will likewise help, if from the first uniting they be often watered, for all moisture helpeth to union. And it is prescribed also to bind the bud as soon as it cometh forth, as well as the stock, at the least for a time.

They report that divers seeds put into a clout, and laid in the earth well dunged, will put up plants contiguous; which, afterwards being bound in, their shoots will incorporate. The like is said of kernels put into a bottle with a narrow mouth filled with earth.

It is reported that young trees of several kinds set contiguous without any binding, and very often watered, in a fruitful ground with the very luxury of the trees will incorporate and grow together. Which seemeth to me the likeliest means that hath yet been propounded; for that the binding doth hinder the natural swelling of the tree; which, while it is in motion doth better unite.

It is evident from the above that Bacon looked upon sexual reproduction in plants as a form of grafting. A famous graft hybrid[5] or chimera was actually secured shortly after Bacon wrote. It originated in Florence in 1644 (Popenoe 1914) and was formed from a union of orange and citron. It was known as the "Bizarria," and an account of it was printed in 1667

[5] Grafting was an ancient practice, and graft hybrids had long been known. An excellent account of them was published by John Baptista Porta in *Magia Naturalis*, Napoli, 1558. This book appeared in numerous editions and was translated into English as *Natural Magick*, London, 1658. The attitude of the sixteenth- and seventeenth-century botanists toward graft hybridization is well illustrated by this work, pp. 58-110.

in the *Philosophical Transactions*. From Vol. I, pp. 553-554:

We have here *Orange*-trees (saith the Intelligence from *Florence*) that bear a fruit, which is Citron on one side, and Orange on the other. They have not been brought hither out of other Countreys; and they are now much propagated by engrafting.

This was lately confirmed to us by a very Ingenius *English* Gentleman, who asserted, that himself not only had seen, but bought of them *In* 1660 in *Paris*, whither they had found an Orange on one branch, and a Lemon on another branch; as also, (constantly to the *Florentine* information) one and the same Fruit half *Orange* and half *Lemon;* and sometimes *three quarters* of one kind and *one quarter* of one other.

Petrus Natus (1675) described the same chimera eight years later (*Phil. Trans. 10:313*). Not everyone believed in the existence of graft hybrids, however, and in certain quarters the accounts were treated with ridicule. Ten years before the record of the orange-lemon graft appeared in the *Philosophical Transactions*, R. A. Austen denied that any such fusion of different species was possible. In *A Treatise of Fruit-Trees*, London, 1657, he treated the matter very lightly. From page 91:

Didymus tells us how we may *mix divers kinds of fruits and thereof make one new kind*. . . . The instruction is too large to show it verbatim: this is the summe. *Two grafts of divers kinds may be cut through the midst, and the two halves bound together, which must be set in the earth, and watered till they bud forth.*

Another to the like purpose. *Binde the Grafts of a Peach-tree and of a Nut-tree together, and the fruits will be halfe Peaches and halfe Nuts:* and *againe* he saies: *Bind the Grafts of a white Fig-tree and a black together, and plant them, and the Figs thereof will have the flesh on the one side white, the other Black.*
Rara avis in terris nigraque similima Cygna.

If men can but make the *Swanne* and the *Raven* breed together, they may have a strange kind of Fowle, a black Swan it may be, which may as soone be done, as to make these fruits mix.

These and the like *instructions* are ridiculous, fit to be passed over with a Jest. . . .

Although spontaneous degeneration offered an explanation of the observed variations in the progeny of hybrid plants, its own *raison d'être* was not accounted for. In *L'academie des Sciences et des Arts*, Paris, 1680, the Reverend Father Leon suggested that the degeneration in tulips was caused by a mingling of different types. From Vol. II, p. 27:

Indeed they [the species] sometimes shift from one to the other. In the time of Xerxes an olive changed into a plane-tree. The domestic fig often degenerates into the wild fig: only rarely does the latter raise itself to the dignity of the former. The *Imperatoire* turns into the *Angelique*, wheat into rye and that into oats. And the diversity of tulips which some believe is caused by a mixing of their bulbs, makes this conjecture probable; that several seeds of different species, crushed and mixed together, would perhaps produce new species as happens among animals.

It is surprising that Leon got this far and no farther, for he knew of the sexuality of plants and actually described pollination in the date palm within three pages of the passage quoted above.

The first real intimation that hybrid plants could be secured by cross pollination seems to have come from Camerarius himself. In the description of the sex of plants in the famous letter to Valentin, he very honestly included some exceptions to the rule he had just discovered, i.e., that pollen was necessary for the production of viable seed. In the absence of all knowledge of apogamy, it was not easy to explain these exceptions. The precise nature of the pollen's action was not realized, and Camerarius suggested that if pollen were just a general fertilizing substance, female plants raised apart from males of their own species could be impregnated by the wind-borne pollen of other species. From *De Sexu plantarum Epistola*, 1694:

I sought to find reason why all plants which flowered late in the field, some few premature ones having already shed their pollen, should be at a distance from each other, or why different species of plant blooming in masses together in the garden, should be covered with dust [pollen], i. e., the female hemp plant which had grown up strongly and joyfully and which needed fertilization; for indeed no one doubts that in the animal kingdom a female can be fertilized by a male of a different species, indeed, as the proverb says, in Africa there is always something new. Also, here again is a difficult question —whether a female plant can be fertilized by the male of a different kind, the female hemp (*Cannabis*) by the male hops (*Humulus*), the castor bean plant (*Ricinus*), from which one has taken the keg-shaped anthers, by being dusted with the pollen of Turkish wheat (*Zea*), etc., and whether a germ would arise from this crossing and to what extent it would be altered. Accordingly I determined to sow the hemp seeds once more and to put the pot in a separate place quite out of the neighborhood of other plants, and I carried out the experiment under these conditions the next summer and I saw that I got by chance just three female plants and the same number of male plants; after I had cut down the latter when they had indeed reached a certain size (for unfortunately I was away) but the anthers had not yet developed, I awaited eagerly the fate of the others. As I had observed earlier in the year, there appeared on the individual plants a huge mass of sterile seeds or empty seminal vesicles without embryos; nevertheless fully formed seeds were present in no small number, and these were the ones attached next to the stalk and the first to develop, while the others developing later were frequently empty and sterile.

From the above it can be seen that Camerarius was interested in plant hybridization as a possible source of evidence for proving that plants reproduced sexually. This was the origin of the real interest in the crossing of varieties and species for the next fifty years.

No account of early hybridization written today could hope to be complete, for there has been too little fundamental search into original sources, unpublished documents, letters,

etc. Many periods of great botanical activity have never been really appreciated, and the records of the work accomplished are completely unavailable. For example, Wang Kuan, a Chinese horticulturist, published a description of thirty-nine varieties of peonies about 1070 A.D. He lived in Yang-chou, which was noted for its peony culture. Accidental hybridization must have occurred here, and possibly there are written records describing it.

The agricultural knowledge of the Cistercians in the twelfth century, when they were draining the swamps of northeastern Germany, has escaped the attention of modern biologists. According to Thompson (1918), they did not just clear the forest land at random, but they knew that where hardwoods grew good land was to be found. They never wholly denuded the forests, but left patches of standing timber. They studied plant life for food purposes, seed germination and the grafting of fruit-trees. Thompson even holds it possible that they practised cross fertilization.

During the seventeenth century there was a great development of new flowers in Japan. The Japanese feudal system required that each noble live near Tokyo a part of every year. The nobles planted flower gardens, and rivalry among them and their gardeners was keen. This was the time of the great Japanese *Iris* culture, when a large number of new varieties were developed. Again, it is highly probable that there was a certain amount of artificial pollination.

Shortly after this development of *Iris* varieties in Japan, the great tulip craze devastated Holland. Some of the Dutch gardeners may have crossed different color varieties, but concealed their knowledge of the function of pollen as a trade secret.

These periods, among others, will have to be studied intensively before we can learn how much was known of plant hybridization before the beginning of the modern era.

III

XENIA IN *ZEA MAYS*

I. THE DATE PALM AND INDIAN CORN

THE dicecious character of the date palm led the Babylonians to the discovery of the rôle of pollen in its fecundation and to a recognition of its sexuality. The next logical step should have revealed sexual reproduction in other flowering plants, for even a superficial examination of perfect flowers would have disclosed pistils, stamens, and the "fertilizing dust." The idea of a combination of both sexes in a single plant, however, would not have harmonized with the philosophical concepts of either the Babylonians or the Greeks. It would mean that vegetables were more "perfect" than animals, and this was unthinkable. Among the many contradictory statements of Aristotle on this subject occurs the following (Vol. VI, pp. 817a-817b):

> The two sexes cannot be found combined in any; if this were so, a plant would be more perfect than an animal, because it would not require anything outside of itself in order to generate; whereas, the plant does require the right season of the year and sunshine and its natural temperature more than anything, requiring them at the time when the tree sprouts.

Fifteen hundred years later this idea of perfection in the vegetable kingdom worried St. Albertus Magnus (*De Veget, et plantis* 1:1:7), and St. Thomas Aquinas in his *Summa Theologica* felt called upon to explain that "the noblest vital function of plants is generation. . . . And among animals there is a vital operation nobler than generation," which granted the reproductive superiority of the vegetable kingdom, but put the plants in their right place. As sexual reproduction was recognized in the date palm but not in other plants, an ex-

planation of the behavior of this unique tree was badly needed. The Arabs in the height of their ascendency supplied the following:

> The palm-tree stands in the highest rank among the plants which come very near to animals, for the palm-tree is an animal-plant, since in its actions and conditions it is different from other plants, although its body remains plant-like. (Brethren of Purity, 900-1000 A.D.)
>
> And the last thing in the vegetable kingdom is the date palm, which has been assimilated to the animal kingdom, since it needs the male to fertilize it so that it may bear fruit. (Nidhami-i-Arudi, 1150-1160 A.D.)
>
> Honor your paternal aunt, the date palm. It was named our paternal aunt because it was created of what was left of the clay of Adam. (Quazwini, 1203-1283 A.D.)

And here the matter rested.

There was a plant in the New World just as important to the inhabitants there as the date palm was to the Babylonians. Indian corn (*Zea Mays*), cultivated from Canada to the Argentine, had been domesticated for so long a time before the arrival of Columbus that its wild ancestor had ceased to exist. The species has separate male and female flowers, but inasmuch as they both occur on the same plant and as many plants are grown close together, wind pollination is effective and nothing can be gained by artificial insemination. The Indians developed many color varieties, and they soon noticed the tendency of the different types to become mixed when they were grown in adjacent plots. Consequently the ceremonial corn, which they wished to keep uncontaminated, was always planted at a distance from other fields. The mixing, they thought, was caused by the fusion underground of small rootlets of different color varieties (Dudley 1724), a reasonable enough explanation, as the natives and even the early settlers knew nothing of sex in plants.

The different colors, which distinguished the several varieties of corn, are located in the endosperm, and hence the grains exhibit xenia, or the direct effect of the pollen upon the seed. As from 300 to 700 grains occur on the single ear, corn is an excellent plant for genetic investigation, and today its hereditary factors or genes are known better than those of any other plant. It was the first plant in which the results of hybridization were clearly recognized (1716), and after a lapse of nearly two hundred years, it served as the basis of a genetical investigation which led to the rediscovery of Mendelism. It is interesting to speculate as to what would have happened if both the date palm, in which the rôle of pollen was discovered, and Indian corn, which shows so clearly the results of cross pollination, had been available to the early old-world civilization.

The first Europeans who examined Indian corn were impressed with the number of color varieties, and they soon noted that different-colored grains often appeared on the same ears. The records they left show that they were not as advanced as the Indians, for they did not interpret this phenomenon as a mixing of different types. At one time each combination of colors was placed in a variety by itself, and the mixture indicated nothing more than the great power of the Deity, whose real purpose in creating such variegated ears was to astonish the inquisitive botanists. Many descriptions of these ears appeared during the sixteenth and seventeenth centuries, and it was not until Cotton Mather wrote to James Petiver that the method of this admixture was described correctly.

2. RECORDS OF XENIA

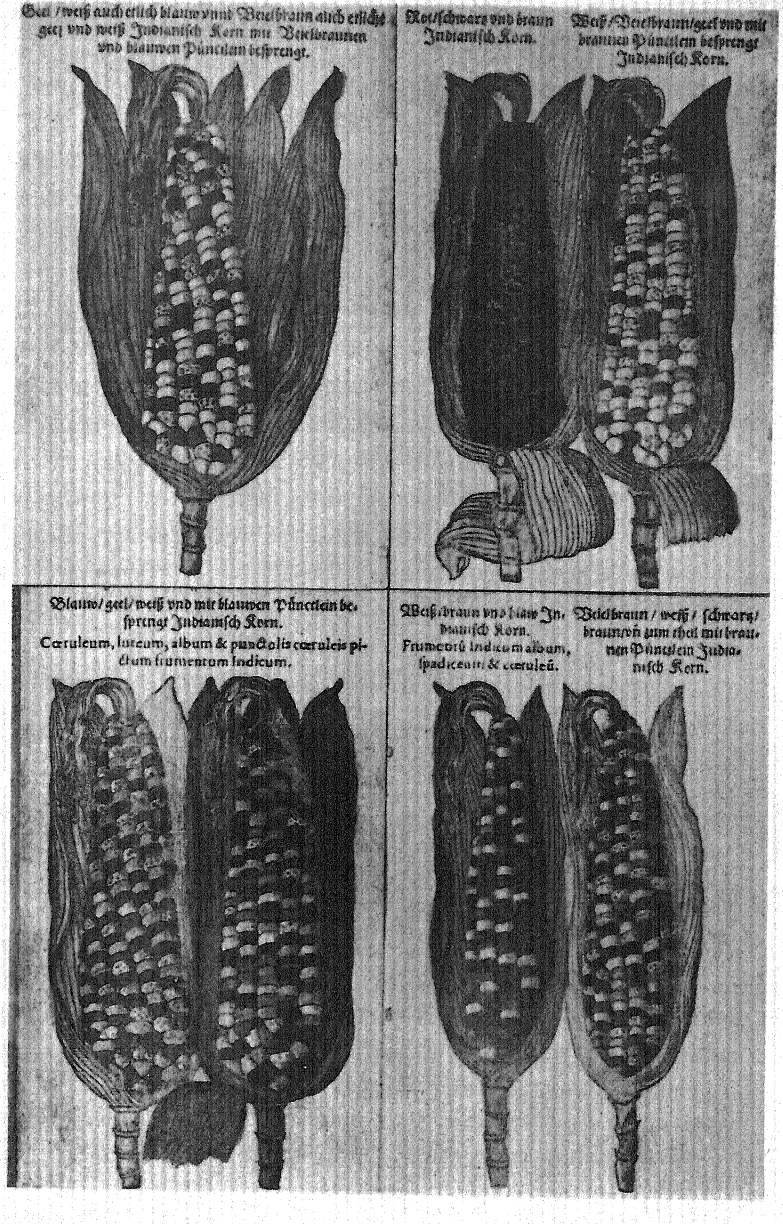
The original sources of many of these early descriptions of Xenia cannot be easily consulted. To complete the record they are here printed in full, even at the cost of a considerable repetition. The remaining portion of this chapter may very

profitably be skipped by anyone not interested in the technical investigation of the genetics of *Zea Mays*.

1. Leonard Fuchs published *De Historia Stirpum* in 1542, and *Prima di Stirpum* in 1549. Both of these contain illustrations of corn, and in a number of copies the illustrations are colored, painted in, probably, shortly after the books were issued. The naked end of an ear which protrudes from the husks on one of the plants is frequently colored in three bands —red, white, and yellow. Although the ear thus decorated bears three types of grain, the regularity of the coloring can hardly indicate variegation. The coloring is probably merely an attempt to make a single figure illustrate three varieties. There is no doubt about the illustrations of Tabernæmontanus, however, as he printed detailed directions for their coloring. Some of his pictures are reproduced opposite. He described the variegated ears with great enthusiasm.

2. Jakob Theodor of Berg-zabern (Tabernæmontanus) published his *Krautebuch* in 1588. The following passage is taken from part I, page 640, under the heading of *Von dem Indianischen Korn:*

> And one sees an especially great and wonderful mystery in these spikes, *Gott der HErr*, through the medium of nature which must serve everyone, disports himself and performs wonders in his works and so notably in the case of this plant that we must rightly be amazed and should learn to know the One True Eternal God even from his creatures alone. For some of the spikes of this plant, together with their fruit, are quite white, some brown-black and dazzingly beautiful, some yellow, some brown, and the others white, brown and blue intermixed. Thus, some rows are half white, a second series brown and the third blue; and some grains, accordingly, are mixed with each other and transposed. Again, sometimes one, two, or three rows are white, the next rows blue, then again white and after that chestnut-brown; that is, they are interchanged on one row and run straight through on another. Some spikes and their grains are entirely yellow, others entirely brown, some are white, brown, and



EARLIEST ILLUSTRATIONS OF MENDELIAN SEGREGATION

blue, others violet, white, black, and brown: of these the white and blue are prettily sprinkled with small dots, as if they had been artistically colored in this way by a painter. Some are red, black, and brown, with sometimes one color next to the other, while at other times two, three, even four colors, more or less, are found one next to another in this way.

Again, some are white, violet, and yellow, and of these the white and yellow are colored with pretty, small brown dots. Again, one finds that the fruit of some spikes is yellow and white. Of these, the yellow and white are sprinkled with violet and blue dots, and, on the other hand, the violet and blue spikes with yellow and white dots. Some spikes, again, are red and chestnut-brown, with here and there one color placed next to the other. Some are blue, yellow, and white, of which the white and yellow are sprinkled with blue dots. So that, as we have said before, one must wonder greatly at this fruit. And (all told) there are fifteen kinds of this Indian corn when all the fruit has colors variegated in this way.

I have seen still another kind of this corn at the house of Herr Stefan Vein, steward of the Elector's Imperial Palace at Libenau, who had it in his garden; . . . The fruit has variegated colors, as white, red, chestnut-brown, yellow, and brown-black, at times with the colors intermixed or transposed; in fact, just as we have indicated them in connection with Indian corn. I should like to have had this plant plucked and set before the eyes of the gracious reader, but at the time I saw this growth I had no painter at my disposal. I shall make amends, however, in time, should *GOtt der HERR* please to continue to grant me this temporal life, which is sealed in his hand and plan.

The illustrations reproduced from Tabernæmontanus are taken from a copy printed in 1613, which is now in the Library of the University of Pennsylvania. It was brought to this country by Johan Ludwig Miller when he emigrated in 1771. Miller was born in Nürnberg, Germany, in 1747 and died in York, Pennsylvania, in 1822. He colored the illustrations of the American plants, probably after he arrived in his new home.

3. P. A. Mattioli described the same phenomena. The German edition of his Herbal, the *Neu Volkommenes Krauter-Buch* was published in Basel, the first edition in 1590. The following quotation is from the edition of 1600. It also appeared in the much later revised edition of 1678.

Indian Corn

They are separated into four varieties. One with brown, the other with light red, the third with yellow, and the fourth with white grains; also another is found containing red, blue, and yellow grains mixed, which appears very amusing.

4. John Gerard published his *History of Plants* in 1597. His illustrations were in part taken from Tabernæmontanus. The following passage is on page 74, under the heading *Of Turkie corne:*

Of Turkie corne there be divers sorts notwithstanding of one stocke or kindred, consisting of sundrie coloured graines, where in the difference is easie to be determined; and for the better explanation of the same I have set forth to your view certaine eares of different colours, in their full and perfect ripeness, and such as they show themselves to be, when their skin or filme doth open itself in the time of gathering.

An illustration is labeled: "Blew and White Turkie Wheate mixed."

5. The New England settlers had not been long in the New World before they were forced by circumstances to take an intense interest in any possible source of food. The European prejudice against maize could not withstand the pressure of real famine. The following passage is taken from *Purchas, His Pilgrims* (Ex. Ser. Vol. 32, p. 317):

A Relation or Journall of a Plantation settled at Plimouth in New England, and proceedings thereof: Printed 1622 and here abbreviated. Wed., Nov. 15, 1620.

We went on further and found new stubble of which they had

gotten Corne this yeare, and many Walnut trees full of Nuts, and great store of Strawberries, and some Vines; passing thus a field or too, which were not great, we came to another, which had also bin new gotten, and there wee found where an house had beene, and foure or five old Plankes laied together; also we found a great Kettle, which had been some Ships kettle and brought out of Europe; there was also a heape of sand made like the former, but it was newly done, wee might see how they padled it with their hands, and found a fine new Basket full of very Faire Corne, some yellow, and some red and others mixt with blew, which was a very goodly sight: the Basket was round, and narrow at the top, it held about three or four bushels, which was as much as two of us could lift up from the ground.

6. Kasper Bauhin published the *Theatri Botanici* in 1620. The following passage is taken from the second edition of 1671, page 24, under the heading *frumentum indicum:*—

Since this corn varies in color of the spikes, Tabernæmontanus represents (pictorially) sixteen varieties and Gerard twelve. These are of both pure and mixed colors. The pure are white, yellow, golden-yellow, violet, chestnut-brown, and black. The mixed colors appear as follows: White and brown; then with blue, white and black partially mixed with brown dots; white, violet, yellow, with brown dots; red, black, and brown; yellow and white, sometimes blue and violet, sometimes yellow and white, sprinkled with violet and blue dots; red and chestnut-brown, golden-yellow and white; blue, yellow, and white, sprinkled with blue dots; and, finally, blue, yellow, violet, and white.

7. Joannes de Laet published *Novum Orbis, seu Descriptionis Indiae Occidentalis* in 1633. The following is from page 7:

Indian maize, which the inhabitants of Virginia call *Pagatowr*, grows in great abundance here and yields grain at times red in color, at times yellow, and at times of mixed colors choicely variegated. It arises to a height of six or seven, and sometimes even ten feet, and bears three or four ears, occasionally, however, only one. These are

loaded with five or six hundred grains, and, when the crop is especially plentiful, even seven hundred; the Indian corn being singular for its luxuriant foliage.

8. Dominque Chabrey in *Stripum icones et sciagrophia,* Geneva, 1666, also noted the mixture of different colored grains. From page 174:

Frumentum Indicum

Formerly of foreign origin, this genus of wheat varies greatly in the color of the flowers and seeds when grown in our region; for the flower color is either purple or red or yellow, so that the color of the future fruits may be calculated. And the fruit is indeed of various colors, at times simple, at others mixed; when of a single color it is white, yellow, violet, or black; when the colors are mixed there are in truth many types of variegated spikes. Gerard describes twelve generations and Tabernæmontanus, sixteen.

9. Erasmus Francisci's *Ost und West—Indisches wie auch Sinnesches Luft-und Stats Garter* was published in Nürnberg in 1668. He likewise described the effects of Xenia in corn, but took his account directly from Tabernæmontanus, including even the pious references to the Deity. Actually, the typographical peculiarities are faithfully reproduced.

10. Abraham Munting mentioned the variegated ears of *Zea* in his *Waare Oeffening der Planten,* Amsterdam, 1672. From page 433:

Frumentum Indicum semine albo, Indian Wheat with a white fruit or seed, *Semine rubre,* with a red fruit, *Semine cœrule* with a blue fruit. Finally, *Frumentum Indicum fructu variegate,* Indian Wheat with a variegated fruit.

11. John Winthrop, F.R.S., a Governor of Connecticut, wrote a paper entitled *"On the Culture and Use of Maize"* which was published in 1678 in the *Philosophical Transactions.* The quotation is from page 1065:

The Ear is for the most part, about a span long composed of sev-

eral, comonly 8 rows of Grains, or more, according to the goodness of the ground; and in each row, usually above 30 grains. Of various colors, as Red, White, Yellow, Blew, Olive, Greenish, Black, specked striped, &c, sometimes in the same field, and the same Ear. But the White and Yellow are the most common. . . .

In the more Northerly parts, they have a peculiar kind called *Mohawks* Corn, which though planted in *June*, will be ripe in season. The stalks of this kind are shorter, and the Ears grow nearer the bottom of the stalk and are generally of diverse colors.

12. Robert Morison first published *Plantarum historiæ oxonensis* in 1680. It was edited after his death by Jacob Bobart and reissued in 1715. The occurrence of different-colored grains on the same ear was recorded in both editions, the last one appearing just one year before Cotton Mather noted the effects of cross pollination:

This corn varies in the color of the spikes and grains. The colors are either pure or mixed. The pure are these: white, yellow and golden yellow, violet, chestnut-brown, red and black. Mixed colors appear in the same spike and sometimes in the same grain. The combinations are: white-brown, and blue, white, black partially mixed with brown dots; white, violet, yellow, with brown dots; red, black and brown; yellow, white, sometimes blue and violet, sometimes yellow and white, sprinkled with violet and blue dots; red and chestnut-brown, golden yellow and white, blue yellow and white, sprinkled with red dots; and finally, blue, yellow, violet and white.

13. Nehemiah Grew did more than any of his contemporaries to popularize the view that plants had sex. Strangely enough he noted the mingling of different varieties of corn without recording any views as to the method of admixture. It seems that Winthrop sent his paper, *The Culture and Use of Maize* to Grew, who in turn submitted it to the *Philosophical Transactions*. Later Grew ran across some variegated ears when he was listing the treasures of the Royal Society. In *A Catalogue and Description of the natural and artificial Rarieties belonging to the Royal Society* published in 1681,

Grew merely listed the ears. From page 222:

Several SPIKES or Heads of MAYS or *Indian*-Wheat; with the Grains, as is not unusual, of three or four colors.

14. John Ray was convinced that the flowering plants reproduced sexually. He also noticed variegated ears, but Mendelian segregation was a phenomenon for which he was unprepared. It seems a trifle ironical that by his observing closely and accurately the growth and development of the color varieties he was prevented by what he found from accepting their hybrid origin. From his *Historia Plantarum* (1686) Pt. II, p. 1250:

Our native Gerard following Tabernæmontanus in error numbered species according to the color of the grains, whereas, most of these varieties could be obtained from the same seed.

15. William Sherard in *Scolia Botanicon*, Amsterdam, 1689, did not follow Ray's interpretation, for he classified the varieties of Zea by their color. From page 261:

Frumentum Indicum Mays dictum *C. B.*, Frumentum Turcicum *Dod.*

Idem granis rubentibus
Idem granis nigri cantibus
Idem granis variegatatis.

16. The *Theatrum Botanicum* of Theodor Zwinger first appeared in 1696. His classification of the color varieties was retained in the later edition of 1744, in spite of the fact that both Mather and Dudley had explained the cause of the mixture of different grains upon a single ear. (From p. 378, ed. of 1744):

It [*Zea Mays*] is separated unto numerous species or kinds. One with brown, another with reddish, a third with yellow and the fourth white and other grains: sometimes even it is found that the red, blue, and yellow grains are mixed together, appearing very beautiful.

17. Joseph Pitton Tournefort named Indian corn *Mays* and

listed a number of varieties in *Institutiones Rei Herbariae* (1700). Among these varieties are:

Mays ears gold and white,
" " white, spotted with chestnut-brown marks,
" " violet-white, spotted with chestnut-brown marks,
" " yellow-white, spotted with violet and blue marks,
" " yellow-white, spotted with red marks,
" " red, black and chestnut-brown,
" " blue, yellow, violet and white.

18. Johann Georg Volckamer published the *Flora Noribergensis* in 1700. His description of Zea is on page 174:

Frumentum Indicum, called Mays, grains of yellow, red, black, saffron, and blue mixed, variegated with red and yellow.

19. Robert Beverly published a *History of Virginia* in 1705. He noted not only the mixture of colors but also of "flint" with "dent."

The late ripe corn is diversified by the shape of the grain only, without any respect to the accidental difference in color, some being blue, some red, some yellow, some white and some streaked. That therefore which makes the distinction, is the plumpness or the shriveling of the grain; the one looks as smooth and as full as the early ripe corn; the other has a larger grain and looks shriveled, with a dent on the back of the grain, as if it had never come to perfection, this they call she corn. This is esteemed by the planters as the best for increase, and is universally chosen by them for planting; yet, I can't see but that this also produces the flint corn, accidentally among the other.

20. Sir Hans Sloane published the first volume of *The Naturall History of Jamaica* in 1707. He described *Zea Mays* on page 105:

Frumentum Indicum Mays dictum

It is of several sorts, being the grain is sometimes yellow, dark red, or whitish, etc., which, because I have seen several of them on the same Stalk, I take to be only varieties.

21. William Salmon's *Herball* appeared in 1710. From page 1253:

Of WHEAT Indian or MAIZE.

II. *The Kinds.* We have but One Species thereof, but some may account them Two, by reason of their Magnitude, which I take to be rather from the Nature of the Soil: a rich Soil affording a very large sort: whereas a poor Soil gives you only a Dwarf kind of Plant: But there is a great Variety in the Colors of the Ears, some being all White, some all Yellow, some all Red and some Blew. And again, some Ears have grains of all those Colors at once; but this difference, we account makes no differing in species of the Plant.

In 1716 Cotton Mather described the actual crossing of varieties of corn in a letter to James Petiver. He ascribed the production of different-colored grains on the same ear to cross pollination. Unfortunately this original description was not published, but a few years later he included an account of this mixing of different types in his book, *The Christian Philosopher*, London, 1721. Paul Dudley also noted this spontaneous crossing and described it in detail. He published his observations in the *Philososphical Transactions* of 1724. In the meanwhile (22.) Giuseppe Monti (1719) had followed the older custom of classifying each color combination as a distant variety, and he retained the classification in the edition of *Catalogi stirpum agri bononiensis* issued in 1729. From page 23:

Mays spikes gold and white
" " red, black and brown
" " blue, yellow, violet and white.

In 1749 Benj. Cooke described the crossing of different colors of corn, and in 1750 Pehr Kalm noted the mixing of red and yellow varieties when they were planted near each other. In 1751 William Douglass also ascribed the mixing of colors to cross pollination.

IV

PLANT HYBRIDIZATION BEFORE KOELREUTER

I. ENGLISH AND AMERICAN BOTANY IN THE EARLY EIGHTEENTH CENTURY

ACCURATE accounts of plant hybridization date from the first half of the eighteenth century. During the preceding twenty-five years the ground had been well prepared by the actual proof that pollen was necessary for the production of viable seed, and by the consequent revival of interest in plant sexuality. The learned world had known for a long while that such plants as the date palm and the papaw required the union of the male and female elements before they could produce offspring, but it was not until Nehemiah Grew addressed the Royal Society in 1676 that attention was focused upon the universal rôle of pollen in plant reproduction. Evelyn (1680), Perrault (1680), Helmont (1682), and Sturm (1684, 1687) continued the work by citing the various instances of plant sexuality, and Ray (1686) greatly developed and extended the doctrine. Camerarius (1691-1694) assembled the real proof of the existence of sex in the vegetable kingdom, and his conclusions were generally accepted, although Tournefort missed the significance of the experiments and Malpighi failed to realize the nature of the floral anatomy which he himself had described. Garden (1693), Valentin (1697), and Boccone (1697) accepted the doctrine of plant sexuality, however, and by 1700 botanists were definitely seeking to prove or disprove the new theory. At this time the production of plant hybrids was considered important chiefly because it proved the existence of plant sexuality.

During this period a great interest in gardening and horticulture developed, particularly in England. The chief industry of the nation was still agriculture, and the aristocrats were vitally interested in improving their estates and, to a somewhat lesser extent, in decorating their parks and lawns. Commercial florists were seeking new varieties to meet the demands of the nobility, and the apothecaries were on the lookout for new medicinal plants. Great numbers of novel flowers and ornamental shrubs and trees were imported from the New World and the science of botany developed rapidly. The outstanding gardeners of the time—Miller, Fairchild, Whitmill and Knowlton—made real scientific contributions and, in coöperation with the more learned but less practised philosophers, they performed experiments which greatly advanced the general knowledge of plants.

This botanical activity extended to the English colonies along the Atlantic Coast of North America. A new country filled with strange and interesting plants had just been opened for exploration, and the botanists of Europe were anxious for specimens. Naturalists such as Mark Catesby and Pehr Kalm visited the colonies and collected plants for the European Herbaria. Alexander Garden (1730-1791), of South Carolina, collected and exported plants, as did John Mitchell (d. 1768) of Virginia. John Clayton (1683-1773), Clerk of Gloucester County, Virginia, assembled the plants which were to form the basis of Gronovius's *Flora Virginica*. James Logan (1674-1751), Governor of Pennsylvania, experimented with *Zea Mays* and proved that it reproduced sexually, while his friend, John Bartram (1699-1777), also of Pennsylvania, exported perhaps more native American plants to Europe than did any of the other collectors. Cadwallader Colden (1688-1776), Lieutenant Governor of New York, collected and described the indigenous plants of his region, and in New England Cotton Mather (1663-1728)

and Paul Dudley (1675-1751), both Fellows of the Royal Society, submitted many botanical contributions to the *Philosophical Transactions*. Most of these botanists kept in close touch with each other; they visited and wrote one another letters and exchanged ideas and specimens.

It is not an accident that during this period many experiments on plant hybridization were made by English and American botanists. Indeed, until Linnæus and his students experimented on crossing various plants, the English and American hybridizations were almost the only ones recorded. This period of genetical investigation achieved a fitting culmination in the systematic and scientfic experiments of the German, Joseph Gottlieb Koelreuter.

2. DESCRIPTIONS OF PLANT HYBRIDIZATION BY *Cotton Mather*

Cotton Mather (1663-1728) has been regarded as the type specimen of the bigoted stupid Puritan. He is better known today as a witch hunter than as a scholar and a scientist. His theological conservatism and his outstanding personality have served as a focal point for the popular mind to concentrate its dislike of all that was unlovely in the puritan philosophy, and as a result, his real character has been very effectively obscured. He was undoubtedly credulous and believed on very scanty evidence much which we now know to be false, but he at least kept in touch with the scientific progress of his time, and contributed what he could to the advancement of knowledge. In his own day he received some recognition, an honorary degree from the University of Aberdeen (1710) and election to the Royal Society (1713). His *Magnalia Christi Americana* (1702) is one of the best sources of New England history. In 1721, in spite of violent popular opposition, he courageously advocated the use of inoculation as a preventive of smallpox.

The observations of Cotton Mather, which should take their place in the history of botany, were described by him in a letter to James Petiver, F.R.S., dated September 24, 1716. This letter was not published in the *Philosophical Transactions*, but passed into the collection of Sir Hans Sloane and thus into the British Museum (Sloane Ms. 4065, fol. 255). Kittredge (1916) summarized the contents of the letter, but it has only recently been published in full (Zirkle 1934).

Mather knew of Grew's hypothesis, that the flowering plants reproduced sexually, and he evidently accepted Grew's conclusions, as is shown by this passage (Mather 1721):

> The *Stamina*, with their *Apices:* and the Stylus (called the *Attire* by Dr. *Grew*) which is found a sort of *Male Sperm*, to impregnate and fructify the seed!

The following letter contains the earliest account of plant hybridization yet found:

Boston, N. England.
24^{d} VII^{m} 1716.

Sir:

Tis high time for me to make you some return, that may express my sense of the Obligations, which your Letters, with what accompanied them, have laid upon me.

Tis a Vast Load, and a somewhat uncommon Variety of Employments, which my Various Capacities at home and Correspondence abroad, impose upon me,—Whereof my Friends are so sensible, that their Candor forever has a pardon ready for me, when at any time I fail of keeping Some, in my compliance with their Expressions.

But I hope now to make some Reparation for my Delay of my Duty, and Endeavour an Entertainment that may find some Acceptance with you. I perceive that Botanic studies are those to which you have more singularly applied your Inquisitive and Ingenious Mind. And now that I may find something which may be a little Relishable for you, after that I have mentioned one or two curious Observations upon some occurrences in the Vegetable Kingdome, I will fulfill a promise which I made unto my most valuable Dr. *Woodward*, a

few weeks ago, concerning *American plants*[1] which I was collecting for you.

In a Field not far from the City of *Boston*, there were lately made these Two Experiments.

First: my Friend planted a Row of *Indian Corn* that was Coloured Red and Blue; the rest of the Field being planted with corn of the yellow, which is the most usual colour. To the Windward side, this Red and Blue Row, so infected Three or Four whole Rows, as to communicate the same Colour unto them; and part of ye Fifth, and some of ye Sixth. But to the Lee-ward Side, no less than Seven or Eight Rows, had ye same Colour communicated unto them; and some small Impressions were made on those that were yet further off.

Secondly: The same Friend had his garden ever now and then Robbed of the Squashes, which were growing there. To inflict a pretty little punishment on the Theeves, he planted some *Guords* among the Squashes, (which are in aspect very like 'em) at certain places which he distinguished with a private mark, that he might not be himself imposed upon. By this method, the Thieves were deceived, & discovered, & ridiculed. But yet the honest man saved himself no squashes by ye Trick; for they were so infected and Embittered by the Guords, that there was no eating of them.[2]

Several Useful Hints relating to Vegetation and Agriculture, may be taken from these Experiments; which I wholly leave to your Sagacity, and that of ye Philosophers to whom you may see cause to mention them.

What remains is, To make you a Tender of Six or Seven plants, Which are here esteemed peculiar to *America*. I have not yet found them in any *European* Herbals; and if you find that I have been mis-

[1] From Cotton Mather's Diary of 1716. "Sept. 12, G. D. What shall I do to render my Kinsman at Newton considerably useful? Employ my Kinsman at Roxbury to make a Collection of *Plants*, peculiarly *American*."

[2] The effect of gourd pollen upon the taste of squash was also described by "J. B." in 1755 (see page 190). It may be interesting in this connection to quote from a letter written by Thomas Jefferson to Philip Mazzei on March 17, 1801. This letter is published in *The Works of Thomas Jefferson* (VIII, 16) edited by Ford. "The seeds which I sent you were of the Cymblings (*Cucurbita vermeosa*) & squash (*Cucurbita melopipa*) the latter grows with erect stems: the former trails on the ground altogether. The squash is the best tasted. But if you will plant the Cymblings and pumpkins near together, you will produce the perfect equivalent of the squash, and I am persuaded the squash was originally so produced and that it is a hybridal plant."

taken, you will pardon my Ignorance, and will accept my Intention. I have preserved the plants, as well as I can in a Book of brown paper; and have presumed so far as to Impose Names upon them; and have added Schedules, declaring the vertues and Uses for which ye Indians have employ'd them, and in which ye English have been also confirmed by their Experience.

I have committed the Book unto the care of an honourable Friend, Mr. *Edward Loyd*, (one of ye Judges,) who will do me the honour to deliver it with his own hand.

This is but a part of the Collection that I intend for you; because this year I unhappily miss'd the Seas[on] of securing several plants unknown to ye European[s] which, if I live to another Season, I will do my best that I may be a Master of them.

In the mean time, I shall not be altogether wanting in my Essayes to yeeld all possible Obedience unto your Commands. And, I hope annually to treat the Royal Society also; with such a Number of Comunications, that if every member of that Illustrious Body whose name stands in ye Catalogue (an Honour not yet obtained for mine)[3] will do but half as much, the stores in your Collection will soon become Considerable.

That the Blessing of Heaven may attend y[our] person, and all your generous Endeavours w[hile] in the world; is in the hearty prayer of,

Sir,
Your most affectionate

Friend & Servtt.
Cotton Mather

Mr. Pettiver

With some slight change in the wording, probably to make it more formal, the passage in this letter which described hybridization in *Zea Mays* and *Cucurbita Pepo* was included by Cotton Mather in his book *Religio Philosophica*, or, *The Christian Philosopher*, London, 1721. None of the historians

[3] Cotton Mather was elected to the Royal Society on July 27, 1713, but, living in America, he could not be personally inducted into membership. The matter was not finally settled until April 11, 1723 (Kittredge 1911).

of botany seem to have noticed the contribution. Murdock (1926) reprinted this version, and the attention of geneticists was called to it by the writer (1932). The following excerpt is taken from Essay XXVI, "*Of the VEGETABLES*":

That I may a little contribute my *two Mites* to the illustration of the way wherein Vegetation is carried on, I will here communicate a couple of Experiments lately made in my Neighborhood.

My Neighbour planted a Row of Hills in his Field with our *Indian Corn*, but such a Grain as was coloured *red* and *blue*; the rest of the Field he planted with Corn of the most usual colour, which is *yellow*. To the most *Windward-side* this Row infected four of the next neighbouring Rows, and part of the fifth, and some at the sixth, to render them colour'd like what grew on itself. But on the *Leeward-side* no less than seven or eight Rows were so colour'd, and some smaller impressions were made on those that were yet further distant.

The same Neighbour having his Garden often robb'd of the *Squashes* growing in it, planted some *Gourds* among them, which are to appearance very like them, and which he distinguish'd by certain adjacent marks, that he might not himself be imposed upon; by this means the Thieves 'tis true found a very *bitter Sauce*, but then all the *Squashes* were so infected and embitter'd, that he was not himself able to eat what the Thieves had left of them.

As the bitterness of the squashes following this misalliance with the gourds appears a generation too soon, it is regrettable that a more careful record was not kept, for we can hardly interpret this account as a well-authenticated instance of metaxenia.

Thomas Fairchild

Thomas Fairchild (1667-1729) made the first artificial hybrid when he fertilized a carnation (*Dianthus caryophyllus*) with the pollen of a sweet william (*Dianthus barbatus*). We do not know exactly when this cross was made. The earliest record we have of it is Bradley's *New Improvements of*

Planting and Gardening, published in London in 1717, and consequently the hybridization must have occurred some time before this date. Although Fairchild's contemporaries gave him full credit for his achievements, Sachs minimized it, and the fashion was set which has lasted unchallenged to the present. Sachs did not even mention Fairchild's name, but merely referred to him as a "Gardener in London." Focke cited Fairchild's successful experiment (pp. 55, 430) but added, "This success in artificial fertilization was neither used for the advancement of science nor does it seem to have given gardeners any stimulus for further research." Pfeffer went even further by stating (p. 265), "*Die wohl früher (1719) ausgeffuhrt Kreuzung sweier Nelken durch Fairchild was ein rein gärtnerischer Versuch, der keine wissenenschaftigen Bedeutung erlangte.*" Strangely enough even the recent English and American historians of botany have failed to combat this completely unfair estimate of Fairchild's contribution.

Fairchild was a commercial florist, who operated a large garden in Hoxton from about 1692 to his death in 1729. He imported a number of new foreign plants and devised methods for growing them in England. He investigated the soil requirements of his importations, and designed new types of stoves and greenhouses. Evidence for this phase of his activities can be found in Louden (1842), Nichols (1817), and Pultney (1790). His garden at Hoxton must have been an important distributing center for new varieties, for many passages in Bradley (1726) list a number of plants which could be obtained nowhere else. Indeed in *A General Treatise on Husbandry and Gardening*, London, 1726, Bradley referred to Fairchild over thirty times, and devoted sixteen pages (Vol. II, pp. 458-473) merely to listing the flowers in the garden at Hoxton with the times of blooming. Fairchild was also prominent among his fellow horticulturists, for he was one of the company of London Gardeners who backed the publication of Miller's *Gardeners' Dictionary*.

Fairchild's real bid for fame, however, rests upon his avocations, upon the experiments he devised to satisfy his own and others' curiosity. His observations were accurate and of crucial importance, but unfortunately he left much of the interpretation to his doctrinaire friends. He really published very little himself, a single contribution to the *Philosophical Transactions* (Vol. 33, pp. 127-129), 1724, and *The City Gardener, London, 1722*. In addition to these, one or two anonymous tracts on gardening are generally assigned to him. As a result of his indifference toward publication, it is necessary for us to piece together a great number of scattered references to his work from the writings of his contemporaries, because, with few exceptions, his most important findings are recorded by others.

Nevertheless, it is not difficult to discover the high regard in which he was held during his lifetime, for the comments on his work are uniformly laudatory. Twice he appeared before the Royal Society with exhibits, and the second time his address was printed in the *Transactions*. His coöperation with Blair is honestly acknowledged by the latter in the preface to *Botanick Essays*, London, 1720: "... Mr. Fairchild's (*whom I have often mentioned, and to whom I owe all the practical observations I have advanc'd concerning the Vegetation*)."

Fairchild distinguished between male and female flowers of *Malus Persica* as early as 1700 (Blair 1720). He also attempted to discover the function of some of the floral organs, particularly the nectary, and he was persuaded that the contents of this gland was in some way connected with fertilization, for he found that those flowers from which he had removed the nectar set no seeds (Blair 1720, Miller 1731). Fairchild's very ingenious experiments with grafting were designed to demonstrate the movement of the sap (*Phil. Trans.* 1724, Miller 1724), and his hybridization experiments helped prove the existence of sex in plants. Fundamental as these experiments were, they were never properly

recorded, and today we have to depend upon the *Journal of the Royal Society*, upon Bradley (1717), Miller (1731), Collinson (1740), and others, for Fairchild's contributions.

We do not know how long Fairchild worked on his Dianthus hybridization. The hybrid itself was propagated vegetatively for over a hundred years. An account of the actual finding of this hybrid has recently come to light (Zirkle 1934) and this account shows that it appeared spontaneously in Fairchild's garden. The discovery is described in the Minutes of the Royal Society (*Journal Book* of the Royal Society, Vol. XII, 1714-1720, p. 411).

February 4th, 1719/20

Sr. Hans Sloane, Vice-President in the chair.

The Minutes being read Mr. Fairchild Gardener at Hoxton had leave to be present.

Dr. Blair communicated an account of several Botanick Experiments made by Mr. Fairchild and others, which serve to confirm the truth of the Dr's Notions about the different sexes in Plants & the manner of the circulation of the Sap as they are explained in his late Book of Botany. . . .

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The other Experiment was made by Mr. Fairchild some years ago. He found a plant in his garden of a middle nature between a sweet william & carnation July flower (a speciment of which was produced before the Society) it grew in a bed where the seed of each of those flowers had by accident been thrown promiscuously, & he takes it to be an heterogenous production from these two different flowers . . . these new sort of plants produce no seed, but are barren like the Mule or other Mongrel animals which are generated from different species.

If this account given by Blair is accurate—and we have no reason to doubt its truth, for Fairchild himself was present when it was delivered—it would seem that Fairchild was at least as casual with his famous "Mule Plant" as any of the

other eighteenth-century hybridizers. On the other hand, Bradley definitely states that the carnation was the maternal parent and that the sweet william was the paternal, facts which could not be learned from the incident as described by Blair. It is true that Bradley had few scruples and was dishonest on several occasions, yet we cannot for this reason entirely discount his testimony. He apparently had nothing to gain by a false description of Fairchild's experiment.

The earliest description of this hybrid is in Bradley's *New Improvements in Planting and Gardening, London, 1717.* Here the identity of the male and female parents are recorded. (Part I, pp. 23, 24):

I believe I need not explain how the *Male Dust of Plants* may be convey'd by the Air from one to another, by which the *Generation* and *Production* of new Plants is brought about. . . . Moreover a curious Person may by this knowledge produce such rare Kinds of *Plants* as have not yet been heard of, by making choice of two *Plants* for his purpose, as near alike in their Parts, but chiefly in their *Flowers or Seed-Vessels;* for example the *Carnation* and *Sweet William* are in some respects alike; the *Farina* of one will impregnate the other, and the *Seed* so enliven'd will produce a *Plant* differing from either, as may now be seen in the Garden of *Mr. Thomas Fairchild,* of Hoxton, a Plant neither *Sweet William* nor *Carnation,* but resembling both equally; which was raised from the *Seed* of a *Carnation* that had been impregnated by the *Farina* of the *Sweet William.* These Couplings are not unlike that of the *Mare* with the *Ass* which produces the *Mule,* and in regard to *Generation,* are also the same with *Mules,* not being able to multiply with their *Species,* no more than other Monsters generated in the same manner.

The problem arises, How are we to reconcile these two divergent accounts? The answer, perhaps, lies in the assumption that they describe two different incidents. It would not be in keeping with Fairchild's character for him to find a natural hybrid and experiment no further. Indeed, five years

after the publication of the earliest description of the Dianthus hybridization he stated in *The City Gardener* that he was continuing his researches upon "the generation of plants," a phrase which at this time often referred to hybridization. Our records can be made to harmonize if we assume that the hybrid first appeared spontaneously and that later Fairchild secured an artificial hybrid by crossing a female carnation with a male sweet william.

Botanists since Sachs have seemingly known of Fairchild's hybridization through the single reference of Bradley's. It is quoted in part by both Green (1914) and Roberts (1929). While this description is better than any other yet found, it is incomplete and should be supplemented by other citations. Bradley (1717) suggests a practical application of Fairchild's discovery (Pt. II, pp. 84-85):

I have endeavour'd to explain how the *Dust* of one Flower will impregnate and enliven the *Seeds* of another, and that from that accidental Coupling the Seeds are so chang'd as to Plants with Blossoms varying from those of the Mother plant. I have likewise shewn why double Flowers seldom bear *Seed*, which I conjecture is because the Male Parts in them are either not perfect, or else are confin'd from Action by the Multiplicity of the Petals. This Consideration leads me to advise the Curious Florists to plant of every good sort of his double Carnations in Beds on a Line in the Middle, and on each Side of them to set at least Two Rows of single ones of choice Colours, and among them some plants of *Sweet William*, and of the *China* or *Indian Pinks*, whcih have such Varieties of odd Colours in them as I shall mention hereafter. The *China Pinks* and the *Sweet William*, bearing single Flowers, as well as the single Carnation, may have Opportunities of communicating their Farina into the Cells of the double ones, and set their seeds, which if they do, we shall not only gather a larger Quantity than we could otherwise expect, but likewise be assur'd of great Varieties from them.

Miller (1731) under the heading CARYOPHYLLUS has added some details to the description of the hybrid:

CARYOPHYLLUS; *barbatus, hortensis, angustifolius, flore* pleno roseo. The Double Rose-colour'd Sweet John *or* Fairchild's Mule . . . these continue flowering for a long time, and are extremely beautiful, especially the Mule, which produces two full Blooms of Flowers, one in *May* and the other in *July*. . . .

This passage remained in *The Gardener's Dictionary* until 1754. Perhaps the best description of the hybrid is to be found in a letter of Peter Collinson to John Bartram, dated July 22, 1740:

An instance we have in our gardens, raised by the late Thomas Fairchild, who had a plant from seed, that was compounded of the Carnation and Sweet William. It has the leaves of the first, and its flowers double like the Carnation—the size of a Pink—but in clusters like the Sweet William. It is named a *Mule*—per analogy to the mule produced from the Horse and Ass.

The article on Mule Plants in *Chambers' Encyclopedia*, London, 1728-1751, was taken almost verbatim from Bradley's account of Fairchild's experiment:

Mules, among gardeners, a sort of vegetable monsters produced by putting the farina fœcundans of one species of plant into the Pistil, or utricle of another.

The Carnation and sweet william being somewhat alike in their parts, particularly their flowers; the farina of the one will impregnate the other; and the seed so enlivened will produce a plant differing from either.—An instance of this we first had in Mr. Fairchild's garden at Hoxton, when a plant is seen neither sweet-william nor carnation, but resembling both equally; this was raised from the seed of a carnation that had been impregnated by the farina of the sweet-william. These couplings being not unlike those of the mare with the ass, which produce the *mule;* the same name is given them, and they are, like the others, incapable of multiplying their species.

The remainder of this article deals with Bradley's own speculations.

When Miller adopted the Linnæan system in 1759 he included the following under the heading, "Dianthus":

3. The Mule, or Fairchild's Sweet William, it hath narrower leaves than either of the former, and is of that Variety called Sweet John: This was said to have been produced from Seeds of a Carnation, which had been impregnated by the Farina of the Sweet William: The Flowers of this are of a brighter red Colour than either of the former, their Bunches are not quite so large, but the Flowers have an agreeable Odour.

When Thomas Martyn revised the dictionary in 1807, the above passage was slightly condensed.

If the following record of the Mule lacks exactitude, its source justifies its inclusion. Erasmus Darwin was not only a poet, a physician, and a grandfather, but also a well-informed botanist. He knew of Fairchild's hybrid and described it in 1781 thus (*Botanic Garden*, Part II, Canto IIII):

> CARYO'S sweet smile DIANTHUS proud admires,
> And gazing burns with unallow'd desires;
> With sighs and sorrows her compassion moves,
> And wins the damsel to illicit loves.
> The Monster-offspring heirs the father's pride,
> Mask'd in the damask beauties of the bride.

Richard Bradley

Richard Bradley (d. 1732) was a voluminous writer on botanical and agricultural topics. His books did much to stimulate the plant sciences, and the numerous letters he wrote and published helped greatly in popularizing the newer knowledge. Incidentally, his various writings constitute the chief source of our knowledge of Thomas Fairchild.

Bradley was convinced of the sexuality of plants and conducted some experiments on tulips in which he noted that castrated flowers bore no seed. For this work he has been given due credit, but his other observations which helped

prove that plants possessed sex have received little attention, although Roberts (1929) and Hawkes (1928) described Bradley's Auricula (*Primula-Auricula*) hybrids. The two following passages from *New Improvements of Planting and Gardening*, London, 1717, record this work:

Pt. I, pp. 22-23.

'Tis from this accidental Coupling that proceeds the Numberless Varieties of *Fruits* and *Flowers* which are raised every Day from *Seed*. The yellow and black *Auriculas*, which were the first we had in *England*, coupling with one another, produced *Seed* which gave us other Varieties, which again mixing their Qualities in like manner, has afforded us little by little, the numberless Variations which we see at this Day in every curious *Flower-Garden;* for I have saved the *Seeds* of near a hundred plain *Auriculas*, whose *Flowers* were of one Colour, and stood remote from others, and that *Seed* I remember to have produced no Variety; but on the other hand, where I have saved the *Seed* of such plain *Auriculas*, as we have stood together, and were differing in their Colours, that *Seed* has furnish'd me with great Varieties, different from the *Mother Plants*.

Pt. II, pp. 100-101.

With these Perfections we may account an *Auricula* to be good, and from such only we ought to save Seeds for sowing and propagating others, if we hope for success; and as a help to our design let us consult the Chapter relating to the Generation of *Plants*, and improve the Variety by placing such Flowers as are of the most different Colours together whilst they are in *blossom;* that so the *Seed-Vessels* of the one may receive the *Dust* of the other, and by that means give us an agreeable mixture of Colours in those *Plants* we raise from Seed; and it would be well worth our Enquiry, whether the Seeds thus Impregnated partake more of the Shape or of the Colours of the *Flowers* of the Mother *Plant;* to be certain of which, the *Plant* you make Tryal of must be castrated of its *Apices*, before they are ripe or burst open.

Bradley's account of hybridization in Auricula is probably correct. He was not so fortunate, however, in his description

of the effect of foreign pollen upon fruits and melons. While it may be true that foreign pollen affects the parthenocarpic fruit of self-sterile varieties, Bradley, in the following passages, certainly carried metaxenia too far:

Pt. I, pp. 24-25.

We may learn from hence, that the *Fruit* of any *Tree* may be adulterated as well by the *Farina* of one of the same Sort, which perhaps may be sickly and of a Dwarf Kind, as by the *Dust* of some other Kind near akin to it, and worse than itself. Now as such Couplings may be very frequent in common *Woods*, so would I recommend the Choice of *Seed*, to be made only from such *Plants*, or *Timber-Trees* as excel in Greatness or other good Qualities, and are far distant from others of meaner Sorts, which might degenerate their *Seeds*, and cross our Expectations when they come to grow up; and this is as necessary to be observed among *Vegetables*, to maintain their good Qualities in the young *Plants* they are to produce, as it is in the Breeding of *Game-Cocks*, *Spaniels*, or *Running-Horses*.

There is but one sort of *Plant* that I know of, which seems to be out of this Danger of coupling with other Sorts, and consequently of either improving or diminishing the Qualities of its *Seeds*, and that is the Mistletoe; the parts of its Flowers are indeed as apt to Generation as those of other *Plants*, but I have never seen any Variety of this *Plant*, or do I know of any other nearly enough related to it to *engender* with it. . . .

Pt. I, p. 22.

By this Knowledge we may alter the Property and Taste of any *Fruit*, by impregnating the one with the Farina of another of the same Class; as for example, a *Codlin* with a *Pairmain*, which will occasion the *Codlin* so impregnated to last a longer Time than usual, and be of a sharper Taste; or if the *Winter Fruits* should be fecundated with the *Dust* of the *Summer Kinds*, they will decay before their usual Time; and it is from this accidental Coupling of the *Farina* of one with the other, that in an Orchard where there is Variety of Apples, even the Fruit gather'd from the same *Tree*, differ in their Flavour and Times of ripening, and moreover the *Seeds* of

those Apples so generated, being changed by that Means from their Natural Qualities, will produce different kind of *Fruits* if they are sown.

Thirty years later Benjamin Cooke (1745-1749) also reported that the flavor and physical aspects of apples were altered by foreign pollen. It is difficult for us to evaluate these records and still more difficult to accept them at their face value. Metaxenia has been proven to exist in pears and dates, but no effects comparable to those described by Bradley and Cooke have been found. Undoubtedly bud sports were not recognized as such by the eighteenth-century hybridizers, and so we do not know to what extent this factor was involved in their conclusions. The passages just quoted were known to Charles Darwin and were cited by him as evidence that the male elements influenced the mother's body (1868). Unfortunately, Darwin was at that time marshaling all such instances in an attempt to prove telegony.

The following quotation also describes metaxenia and illustrates a belief which is held even today by many practical gardeners: Pt. III, p. 114.

For the more certain producing *Melons* of a right flavour, let me advise that no *Cucumber Plants* be set near them, lest the *Male Dust* of the Cucumbers should happen to be carry'd with the *Wind* upon the *Blossoms* of the *Melons*, and perhaps set them for Fruit which will then certainly give the *Melons*, so produced, the Relish of the *Cucumber* in proportion as the *Farina* happens to fall in greater or lesser Quantity.

Bradley was also interested in hybridizing wall flowers and planned to make some experiments, which probably were never carried out, as no records of them have yet come to light. The following quotation may be taken as a preliminary announcement: Pt. II, p. 91.

The Seed-Vessels of this and other single Kinds of it, as well as their flowers, are so like those of the *Stock July-Flowers*, that I am

of Opinion they might be made to impregnate each other's Seeds if they were planted nigh enough together, and from such Coupling, perhaps, might be produced a *Stock July-Flower* with Yellow Blossoms. It is what I design to try, myself, as well as many other Couplings of the like Nature; and altho' the Seed of such a neutral *Plant* would not be made to grow, the Species may be continued and increas'd by planting *Slips* or *Cuttings* of it, as is common in the culture of *Double-Stocks*.

It is very easy for us to underestimate Bradley's scientific contribution. It is true that his actual experiments were neither well planned, extensive, nor adequately controlled. Nevertheless his numerous writings were very stimulating, and his influence upon the botanists of the early eighteenth century was undoubtedly beneficial. Even when his contemporaries did not agree with his views they were compelled to treat them with respect. More can be found on hybridization and sex in plants in Bradley's works than in the botanical papers of any other man of his time. Bradley was also the chief authority on botany cited by *Chambers' Encyclopedia* and by many other popular educational works. However, one investigator, John Laurence, Rector of Yelvertoft, could not accept Bradley's speculations in the absence of experimental proof. In *A New System of Agriculture*, London, 1726, he quoted Bradley's directions for securing new varieties of carnations through hybridization, and then took a sly dig at the author. From page 427:

Doubtless Mr. *Bradley* having since this first Conjecture, had many years wherein to try his Experiments, and to improve Vegetables, will quickly give us a History of his Success, and a Catalogue of new Fruits as well as new Flowers.

On the other hand, Noël Antoine Pluche accepted Bradley's results and cited him as an authority in the *Spectacle de la Nature*, Paris, 1732. This work was translated by Samuel Humphreys, and published in London, 1736-1737, under

the title *NATURE DISPLAYED, being DISCOURSES on such Particulars of NATURAL HISTORY as were thought most proper to Excite the CURIOSITY, and FORM the Minds of YOUTH.* Youth was to be entertained as well as instructed, and the acquisition of dry facts was to be rendered almost painless by imbedding them in dialogues between nice people. The participants in these conversations were the Count de Jonval, his Countess, the Chevalier du Breuil, and the Prior de Jonval. This choice of characters enabled the author not only to show what Counts, Chevaliers, and Priors talked about in their spare moments, but also to demonstrate that most people were interested in the subjects which young fellows learned from their tutors. The English gentleman referred to in the following dialogue is Mr. Bradley. From Vol. II, pp. 38-40:

Chevalier: Is there not some other Advantage to be gain'd from the Pots, which are capable of being removed where we please?

Count: What may that be?

Chevalier: We might place the Flowers as near to each other as we should think fit, in order to diversify the Colours of those which are to spring from their Seeds; and possibly to preserve the most amiable of the Tribe, from any Intermixture or Variation, from Year to Year, by disposing them apart from others.

Count: In what manner do you conceive, that one Flower makes any Discovery, or not, of its Neighborhood to another?

Chevalier: An *English* gentleman happen'd, yesterday, to pass this Way and having heard some account of your Lordship's flowers, expressed an Inclination to see them. The Prior and myself, were much delighted while we entertained him; and he assur'd us, he was persuaded that the Powders, which fall from the tops of the Chives, are frequently wafted to some distance, by the Motion of the Air; and that by their action on the Pistil, or Style, of another Flower of the same Species, but of a different Colour; they impregnate some of its Seeds, and diffuse a new Tincture into the Colours of the Flower, which springs from that Seed.

Count: This Observation may, in my Opinion, be Justified by many surprising Varieties, that are discovered every Year, in the Flowers raised from the Seed of those which are ranged together on a Theater or reared in the same Bed.

Chevalier: Our *English* Gentleman acquainted us with another Particular, which may possibly be very useful, were the Experiment certain. He assured us, that when he had cut the Chives off several Flowers, before their first Opening, he placed those Flowers at a distance from the rest, and had never observed them to produce the Chives of some others, and left them in the common Bed, with their Companions, he found them all impregnated with Seeds, which undoubtedly, were imparted by the neighboring Flowers. He likewise observed, that after he had cut the Chives of a Flower when it was first unfolded, he scatter'd on the Heart or Style, the Powder of another Flower of the same Species, that was fully blown, and which created a remarkable Change in the Flower he had deprived of its Seed. But he surprised us extremely when he added, that the same experiment made on Flowers, which entirely differ'd from each other in their Nature and Qualities, produced Seeds; and that the Flowers which sprung from them, were composed of those different Qualities: but he assured us, that these new Flowers, which had no Similitude to any others he had ever seen before, were unproductive of any Seed, the next Year, and not perpetuated like the rest.

Count: Were this Fact certain, it would have some correspondence with the Birth and Sterility of Mules, who may be considered by us as Monsters, because they are the Offspring of Animals, who not only differ in Species, but likewise in Nature. But repeated Experiments must inform us of the Consequences and Practice that may be derived from a clear knowledge of the Structure of Flowers.

Chevalier: I intend to make all these Experiments, with as much Circumspection as possible.

Count: I am pleased with your Curiosity: Be sure to cut a number of Chives, and inform yourself, by all the Tricks you can invent; neither your Time, nor your Money, will sustain any Risk by this Proceeding. I think I have some Experience in the management of Gardens, but shall be charmed to receive any Information from you.

And though I am far from resigning my Judgment to the first plausible Idea, presented to me by other Persons, Yet I think it is a criminal Presumption to be so tenacious of one's first Knowledge, as to dislike any mention of new Discoveries. We are still in the Infancy of Arts.

Jean Marchant

Jean Marchant (d. 1738) did not contribute much to our knowledge of plant hybridization. He observed what was probably an instance of Mendelian segregation in Mercurialis, without, of course, understanding what he saw. As this plant is dicœcious, and as both segregants in the first hybrid generation were of the same sex, variety crossing probably occurred. We cannot be positive, however, for Marchant's description is somewhat vague. He knew that the two sexes were separated in the plants which he was observing, but he was mistaken in his identification of the sexes, calling the male, female and the female, male. Possibly the reappearance of the segregant in subsequent generations was due to the heterogeneous condition of the original stock, and not to a continued back crossing of the aberrant type. Marchant's work was known to Linnæus and his students, and it is cited by both Rudberg (1744) and Haartman (1751) as a record of plant hybridization.

In July 1715, Marchant found what appeared to be a new variety of Mercurialis growing in his own garden. The next April six other plants appeared in the same place, four like the plant of the previous year and two different from the parent type. The two segregants were male plants (Marchant called them female) and in the following years both types of plants reappeared. Marchant announced his find in the *Historie de l'Academie Royal des Sciences de Paris* for the year 1719, which was printed in 1721. In describing the appearance of new types, he showed that he was particularly interested in the origin of species. From pp. 63-64:

These two Plants are annual, nevertheless they last much longer than the common "Mercurialis" since they have been seen to germinate at the beginning of April and since they stay green until the end of December.

They are very much alike in their flowers, their taste, and the consistency of their leaves, but they differ exceedingly in their habit, and in the shape of their leaves, as has been said.

The common opinion among Botanists is that the male *Mercurialis* bears seeds and never forms flowers, and that its seeds produce indifferently the two kinds of *Mercurialis*, as many male as female; whereas the female Mercurialis bears only sterile flowers, that is to say, that it never furnishes seeds.

According to this principle our two new Plants whose flowers we have seen were female *Mercurialis*, coming from the seeds of the male Mercurialis; but then it is rather hard to understand why these Plants come up again just in this Garden only in the space of seven or eight feet of ground where they were discovered for the first time, seeing that the male and female of the common *Mercurialis* germinate and come up again in great abundance in all the Gardens; that makes it seem, contrary to the sentiment of modern Botanists, that the two Plants which we describe here, bear seeds, since they reproduce themselves in the same form in this place, certainly they are never found elsewhere.

We will continue our observation on this phenomenon; meanwhile we will propose certain conjectures on the multiplicity of species which we believe that Plants can engender.

The Physicians who apply themselves to Gardening, particularly those who love Plants that bear beautiful flowers, like Anemones, Tulips, Carnations, & other flowers, know perfectly that the seeds of these Plants, being sown, are often of agreeable or curious diversities. Nature, without having regard for the beauty of flowers, uses them thus in the diversity of species which she multiplies in the Herbs or Simples.

The example of our two new Plants shows it well enough, since in four years we see born two constant species which were unknown to us. Through this observation the suspicion would arise that the All-Powerful having at one time created individuals of Plants for a model

of each genus, made in all structures and characters imaginable, fit to produce their like, and these models or heads of each genus, in perpetuating themselves, might finally have produced varieties, among which those which remained constant & permanent have constituted species, which by succession of time and in the same manner have made other different productions, which have so multiplied Botany in certain genera, that it is certain that we know today in some genera of Plants up to one hundred, one hundred and fifty, & even up to over two hundred distinct and constant species belonging to a single genus of Plants.

The truth of what is advanced on the subject of the production of species, appears the better founded since it is known that the most ancient Botanists have mentioned only about four hundred heads of genera of Plants, to which they add few species, which makes us think that at that time the species were not yet very numerous; while we know at present more than eight hundred heads of genera, burdened with thirteen to fourteen species or more, among which, truly, many are repeated & others are only simple varieties.

Thomas Knowlton

Thomas Knowlton was born in 1692. As a young man he was a gardener in the service of William Sherard. On the death of Sherard in 1728 he entered the service of the Earl of Burlington and moved to Lanesbrough in Yorkshire. He died there in 1782. He was a friend of a number of the best botanists in his day, among others Sir Hans Sloane, Patrick Blair, Mark Catesby, and, of course, William Sherard. Knowlton is known as the discoverer of the Moore Balls or Globe Conferva (*Conferva Ægagropila Lin.*). He also had several letters published in the *Philosophical Transactions* (1746). In these communications he described the discovery of the ruins of the ancient Roman town, Delgovicia, and the finding of some horns of extinct species of deer. A genus of the Ranunculaceae is named for him.

Knowlton's observations on hybridization and sex in plants

were reported by Patrick Blair to the Royal Society in 1720, at the same meeting in which Fairchild's Mule Plant was exhibited. The following extract is taken from the Journal Book of the Royal Society, Vol. XII, pp. 411-412:

Mr. Knowlton Gardener at Offly place in Hertfordshire took two parcels of Turkey wheate. He put the grains of one of these parcels into the ground singly grain by grain, the other parcel he sow'd in Drills promiscuously after the usual manner.

That which was sown singly shed its dust before the female embri began to appear & most of it miscarried. The few seed which ripened, he committed to the ground in September but it produced nothing. The other parcel of wheat ripened very well & produced plentifully 3 or 4 ears each Stalk with 10 or 11 Rows of Seed in each ear. This confirms what is laid down in the 238 & 239 page of his [Blair's] Book of Botany. That the union of male & female flowers are necessary to fructification.

In regard to the crossnig of species, Blair cites the Dianthus hybridization of Fairchild already quoted (p. 110) and then adds:

The like has been observed by Mr. Knowlton who found a new plant partaking of the natures of a China pink & sweet william. And they both observe that these new sort of plants produce no seed, but are barren like the Mule or other Mungrel animals which are generated from different species.

Philip Miller

Philip Miller (1694-1771) became the head gardener of the Chelsea Physic Garden in 1722, a post which he held for the next forty-five years. He imported a number of new plants, greatly increased the Chelsea collection and made the Physic Garden a real botanical center. He corresponded with many of the scientific leaders of his time—Blair, Bradley, Sloane, Bartram, Linnæus, and others—and consequently a number of his letters have been printed. He was, perhaps, the most widely known botanist of his generation, for in his

PHILIP MILLER

own lifetime his *Gardener's Dictionary* passed through eight full and six abridged editions, together with editions in French, Dutch and German. This famous *Dictionary* appeared first in 1724 in octavo and in 1731 in folio. Most of his contributions appeared in the various editions of this work.

Strangely enough, Miller's discoveries have been in part overlooked. He is credited with noting that when female spinach plants were grown apart from the males, they produce seed which contained no embryos. He was also the first to discover insect pollination. Sachs recognized Miller's discovery but dated it 1751, the year in which the German edition of the *Dictionary* appeared. This would make Miller's observation later than Wahlbom's (1746), who also noted that "bees do more good than harm for they scatter pollen on the pistil."[4] The English historians of Botany have quoted from the earlier editions of the *Dictionary*. Miller actually performed his experiments and reported his observations earlier than our current records would indicate, for on October 6, 1721, he wrote a letter to Richard Bradley describing the insect pollination of Tulips and the sterility of unfertilized spinach flowers. On November 11, 1721, he sent another letter to Patrick Blair, which also included a description of these observations. The letter to Bradley was published by the latter in his *Treatise on Husbandry and Gardening*, London, 1726; Blair sent his letter to Sir Hans Sloane, who published it in the *Philosophical Transactions*, Number 369.

Miller also reported sexual reproduction in cucumbers and melons, and described hybridization in Brassica. These accounts appeared in the dictionary, but an earlier record is contained in a letter written to Patrick Blair dated October 19, 1721. This was also sent to Sir Hans Sloane and published by him in the *Philosophical Transactions* (31:215-224):

[4] Julius Pontedera wrote a letter entitled *De stirpum fœcundatione apicibus attributa* in 1755. This was published in his *Epistula et Dissertatio*, Patavi, 1791, as Epistle IX.

Observations upon the Generation of Plants, in a letter to Sir Hans Sloane, Bart Pr. Coll. Med. Patrick Blair, *M.D., F.R.S.*

Boston, Dec. 31, 1721

Honoured Sir:

It is no small Satisfaction, that what I advanced in my *Botanick Essays* is now so fully confirm'd by Experiments made by some curious Gardeners, among whom is Mr. *Philip Miller*, who writes me. . . . By a Second Letter, *October* 19, 1721, he informs me, that he bought a Parcel of *Savoy* Seeds of a Neighbor, which he sowed, and planted out the Plants; but was surprised to see the Production: For he had half of them red Cabbages, and some white Cabbages, and some Savoys with red Ribs, and some neither one Sort nor other, but a Mixture of all Sorts together in one Plant. He went to the Gardener and told him his Tale, who shew'd him, that he was in the same condition, but did not know how it should come to pass, for he was sure he took special Care in saving of the Seed. Being ask'd how and where he planted them for Seed, he shew'd him them under a *South-West* Hedge, and told him the Manner in which he planted them: First, a Dozen of white Cabbages, then a Dozen of Savoys, and then a Dozen of Red. Then he immediately thought how it came to pass, by the *Effluvia* impregnating the *Uterus* of one another; and it is very common for our Gardeners to plant white and red Cabbages together for Seed, and they are as often disappointed by having a Degeneracy of both Kinds, which they attribute to the Soil, and think that is the Cause: They send to *Holland* for a fresh supply of Seeds, and say our Soil will not continue that Sort Good. He told them his Opinion, and they laugh at him for it, and will not be turn'd out of their Road, although they should have never so many Experiments shew'd them.

The philosophical Blair commented upon Miller's experience as follows:

This Experiment is a most convincing Argument for the *Effluvia;* for did each Grain of the *Farina* enter the *Pistilum* to its proper *Uterus,* this mongrel Kind would never be produced. For if the individual Plant be in each Grain of the Male *Farina,* how can it be so

far dismember'd, as that one Part shall go to the making up of the Ribs of red Cabbage, and another to compose the rest of a Savoy Plant. Analogous to this, is what I lately observ'd in a Spaniel Bitch, of so good a Kind, that when she became proud, Care was taken to let her have good Dogs. The litter she produced, consisted of Puppies some Piebald, like one of the Dogs that had lin'd her, of the same Shape, Colour, and Spots; others like another; and a third partaking of both, with Spots from the Bitch interspers'd. This is a farther Confirmation of what I have advanc'd, Essay 4. where (Page 310) I only assert, that several Fœtus's partake equally of Male and Female; but here two Males concur with one Female in the Composition of a fourth Body, made up of all the three: And one Seed produces a Cabbage consisting of three different Species, which could never happen, did these organiz'd *Animalcula*, or Granules of the *Farina*, become a *Fœtus*, or contain the *Folia Seminalia* of a Plant. This methinks is sufficient to answer what the ingenious Mr. Bradley has so strenuously contended for, *Works of Nature, p. 9. & Seq.* But since that worthy Gentleman has not thought fit to answer what I have already advanc'd upon that Subject, I may hereafter answer his Objections more at large.

I could descant yet more upon this Observation, and consider how far this may lead us into the infinite Variegations and Stripes, in not only annual Flowers, such as Poppies, *consolida Regalis*, and Bottles, but also in perenial Roots; such as Auricula's, Cowslips, & of a lower Size, which is hinted by Mr. *Bradley*; he having received that Notion from the ingenious Mr. *Du Bois*, as I have been credibly informed; and in Plants of a larger Size, not of a Bulbous, but Carnous Root, such as Columbines; where there is a vast Variety: And in this Plant it is most especially to be observed, that though the indigenous one, from which all the other seem only to be Variations, and not determinate Species, be of a blue Colour, consisting of ten Alternate Petala, viz. five corniculate, and five plain; yet into how many other Kinds of Flowers is it subdivided; such as pale yellow, with bluish red, purple, dark Stripes vastly double, blue, blackish red &c. Some with Corniculate *Petals*, and some only with plain, and how in single Flowers it imitates all the Colours we see Pigeons endow'd with.

I say it is worthy of consideration, whether the *Farina* may do this, since I do not understand there has been much Art used in making these Flowers break, as Tulips, or to cultivate a Set of Breeders; but that a richer Soil may produce a double Flower; and a suitable Loam may produce the Variety of Colours; the *Farina* from several Flowers may occasion the Stripes, and the Stamins arising from the plain *Petals*, rather than the *Cornicula*, pouring out the *Farina*, may cause the Flowers with the plain *Petals*. So that were I to extend this to a great many other Plants, and were there proper Observations made upon them considerable Improvements might be made upon this Doctrine of the Sexes of Plants. For after the Flowers, we come next to the Variegation of the Seed of some Plants, particularly the *Phaseoli*, whose various Spots and Colours, and even the Bigness too, may very much depend upon the *Effluvia* from the *Farina*, when several Kinds are sown together. For do but consider three plain Colours, a White, Red, and dark Blue, and you may observe how many Descendants, and what a Variety of Spots may proceed from them. The lupines also in some Measure may be brought in here, and I know not but that the *Medica Cochleata Falcata Lunata* may be multiply'd in its Variations after the same Manner.

Miller also described the hybridization of *Brassica* in an article entitled "Generation," published in the *Gardener's Dictionary*. From the edition of 1733:

In a Parcel of *Savoys*, which were planted for Seed near white *Cabbages*, the Seeds when sown, produc'd half red, and some white *Cabbages*, and some *Savoys* with red Ribs, and some neither one Sort nor the other, but a Mixture of all Sorts together in one Plant, which I suppose might happen by the *Effluvia* impregnating the *Uterus* of each other.

Some practical directions were given in the article on *Brassica*. From the same edition:

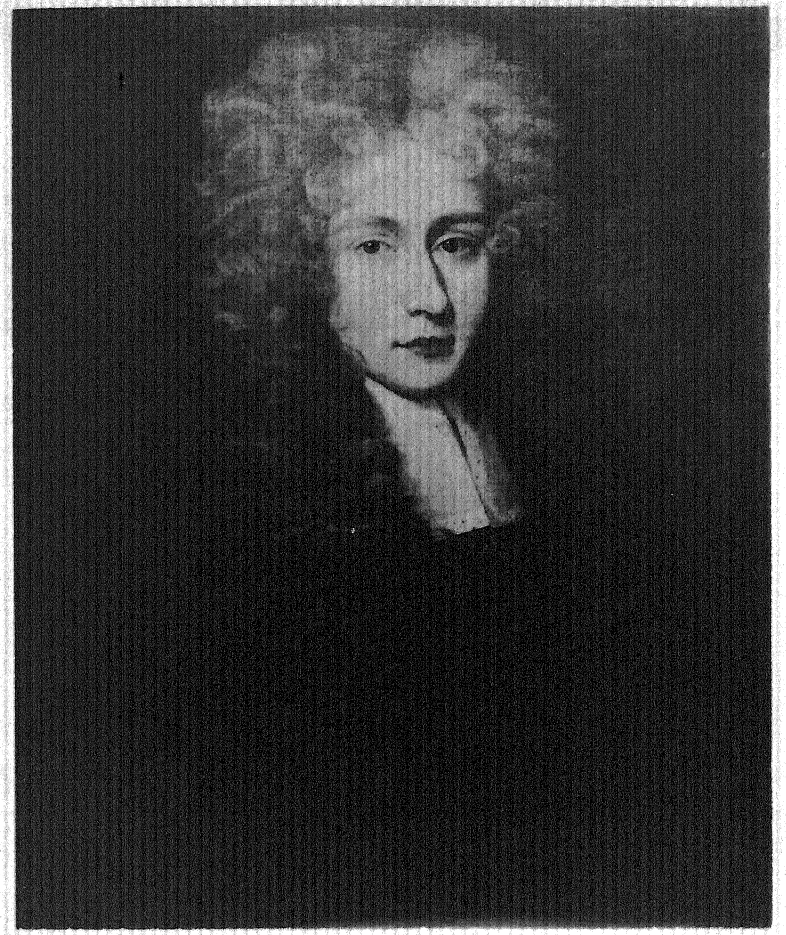
But in planting of Cabbages for Seed, I would advise never to plant more than one sort in a Place, or near one another. As for Example: Never plant *red* and *white Cabbages* near each other, nor

Savoy with either *white* or *red Cabbages*: For I am very certain they will, by the Commixture of their *Effluvia*, produce a Mixture of Kinds: And it is wholly owing to this Neglect that the Gardeners rarely save any good *red Cabbage-Seed* in England, but are obliged to procure fresh Seeds from abroad, as supposing the Soil or Climate of *England* alters them from Red to White, and of a mix'd Kind between both, whereas if they would plant *red Cabbages* by themselves for Seed, and not suffer any other to be near them, they might continue the Kind as good in *England*, as in any other Part of the World.

Paul Dudley

Paul Dudley (1675-1751) was a member of a distinguished Massachusetts family. In 1702 he became Attorney-General of the Colony, and in 1718 a Judge of the Superior Court. He was an excellent naturalist and a Fellow of the Royal Society. Although his legal affairs and his poltical duties consumed the major portion of his time, he was able to pursue his studies in natural history, and he submitted many contributions to the Royal Society, which were printed in due course in the *Philosophical Transactions*. In 1724 he published "Observations on some of the Plants in New England, with remarkable Instances of the Nature and Power of Vegetation," *Philosophical Transactions* 33: 194-200. It was in this article that he gave an account of hybridization in *Zea Mays*. This work of Dudley's was the basis of all of Miller's description of variety crosses in *Zea* which appeared in the *Gardener's Dictionary*. Miller quoted from Dudley's paper in two different articles "Generation" and "Mays: Indian Wheat." Dudley's contribution to the discovery of plant hybridization has been missed by most of the historians of botany. Weatherwax (1923), however, quoted the work from the abridged edition of the *Philosophical Transactions* 7: 57-61, London, 1809, and the writer (1932) recently reprinted Dudley's original report. Otherwise, this record of hybridization seems to have escaped notice.

The mention of *Indian* Corn obliges me to take notice of an extraordinary *Phænomenon* in the Vegetation of that Grain, *viz.* the interchanging, or mixing, of Colours, after the corn, is planted. For your better understanding of this Matter, I must observe, that our Indian Corn is of several Colours, as blue, white, red and yellow; and if they are planted separately, or by themselves, so that no other Sort be near them, they will keep to their own Colour, *i.e.*, the Blue will produce blue, the white, white, *etc.* But if in the same Field, you plant the blue Corn in one Row of Hills (as we term them) and the white, or yellow, in the next Row, they will mix and interchange their Colours; that is, some of the ears of Corn in the blue Corn Rows, shall be white, or yellow; and some again, in the white or yellow Rows, shall be of a blue Colour. Our Hills of *Indian* Corn are generally about four Foot asunder, and so continued in a straight Line, or Row of Hills, and so on; and yet this mixing and interchanging of Colours has been observed, when the Distance between the Rows of Hills has been several Yards; and a worthy Clergyman, of an Island in this Province (*The Reverend Mr.* Mayhew, *of* Martha's *Vineyard*), assures me that the blue Corn has thus communicated, or exchanged even at the Distance of four or five Rods; and, particularly in one Place, where there was a broad Ditch of Water betwixt them. Some of our People, but especially the *Aborigines*, have been of the Opinion, that this Commixtion, and Interchange, was owing to the Roots, and small Fibers reaching to and communicating with one another; but this must certainly be a Mistake, considering the great Distance of the Communication, especially at some Times, and cross a Canal of Water; for the smallest Fibres of the Roots of our Indian Corn, cannot extend above four or five Foot. I am therefore humbly of Opinion, that the *Stamina*, or Principles of this wonderful Copulation, or mixing of Colours, are carried thro' the Air by the Wind; and that the Time, or Season of it, is when the Corn is in the Earing, and while the Milk is in the Grain, for at that Time, the Corn is in a Sort of Estuation, and emits a strong Scent. One Thing, which confirms the Air's being the Medium of this Communication of Colours in the Corn, is an Observation of one of my Neighbours, that a close, high board Fence, between two Fields of Corn that were



PAUL DUDLEY

of a different Colour, entirely prevented any Mixture or Alteration of Colour, from that they were planted with.

Henri Louis du Hamel du Monceau

Du Hamel (1700-1782) certainly did not add greatly to our knowledge of specific plant hybrids, nor did he base his first contribution on any of his own experiments. Nevertheless his paper, *Recherches sur les causes de la multiplication des espèces de fruits* (June 30, 1728) published the year of his election to the Academy of Science, showed that he had a clear grasp of the essentials of hybridization and that he foresaw its practical application to the improvement of economic plants. He also noted the bearing of hybridization upon the problem of the origin of species, and, together with Marchant, he deserves to be ranked with the pre-Darwinian evolutionists. The following quotation is from pages 490-497 of his essay:

But we see changes much more essential, more unexpected and more constant than can be effected in any manner by Art. One must then seek another cause.

I would wish, after having renewed a difficulty, to be in a position to give a correct solution: but I do not propose here to report those conjectures which by their simplicity and nature have seemed to me to deserve attention.

Among the groups of authors who have examined the structure of plants there are both ancients and moderns who, with much semblance of truth, compare the multiplication of plants with that of animals, that is: they make the reproduction consist of a union of the two sexes, whence results the fertilization of the eggs, which then needs only a certain degree of warmth and moisture for the parts of either the animal or of the plant, of which it is the origin, to develop and acquire length. To relieve myself of reporting how those, who have held this sentiment, have explained it, I will state that one may get enlightenment from the discourse of Camerarius, *du Sexe des Plantes*, from the Memoir of M. Geoffroy, the younger, on the structure of

flowers, and from that of M. Vaillant. I content myself with showing that this sentiment is not new, and with recounting a passage from Pliny and from Jonston. Here is the way the first of these authors explains it: "*Veneris intellectum maresque afflatu quodam et pulvere etiam fœminas maritare.*" And Jonston: "*Maritare quasdam necesse est, hinc maris et fœminae confusa in illis principia sunt.*"

It is by following this comparison that I have believed it possible to explain the varieties which are found among plants by those which one notices so often among animals: so just as from the coupling of two kinds of dogs there comes one which takes after both, to which has been given the name *Mety*, in the same way, when the wind has carried the dust from the stamens of some kinds of pears for the pistil of another, there will result a seed whose germ takes after both.

To understand the truth of this conjecture it is sufficient to notice that almost all the fruits that gardeners call *new* are only composites of other older ones which can be recognized easily: here is an example: The *Colmard*, which capable gardeners say has come from a pip of *Bon-chrètien*, is only a composite of *Bon-chrètien* and of *Autumn-Bergamotte*. Whence comes this analogy? Whence comes this resemblance?

I am constrained to believe that the *Colmard* may have come, as our gardeners think, from a pip of *Bon-chrètien*, but made fertile by a *Bergamotte*, a thing which can happen very easily in the orchards where all species are mixed up, but less easily in the woods where this mixture of species is not found so commonly; thus one notices that they are more constant in their production than are those of our gardens. If one tastes the fruit carefully, one might find a number of qualities like those of the *Colmard*. One must admit meanwhile that there are fruits of a taste and sap so extraordinary that it would be difficult to relate them to known species. I do not believe, however, that one could draw from this observation an argument capable of destroying that conjecture, since the mixture of two saps can produce a strange composite, perhaps can even occasion a fermentation which disguises them totally.

There are even fruits where this mixture is imperfect, with the result that the kinds are sufficiently distinct to make it possible to

eat a quarter of a fruit separate and distinct from that with which it is joined; thus there is among the oranges the hermaphrodite or the monster which on the same tree produces the *Bagarade*, the *Citron*, and the *Balotin* separately, on different branches or united and assembled in the same fruit. So also is that kind of grape which produces on the same vine red and white clusters, on the same cluster red and white grapes, or whose seeds are half red and half white. I have not yet been able to convince myself that the reasons which the authors give us for obtaining these species of trees are true, which is why I dare not suspect (hint?) the cause of these varieties, in the mixture of dusts, although we may see every day in the same litter dogs which resemble the mother entirely, others the father, others both, and even others which have characteristics of both so distinctly that one-half of their body resembles the father and the other the mother: but experiences speak for themselves, and we should take care to relate to the Society whatever might be successful and enlightening to them which we have been able to draw from this.

I believe that one can avail oneself of this conjecture to explain the infinite variations which happen in certain genera of plants, since they are so very frequent, that the different species of a single genus are augmented to a very great number; this shows why certain plants in the field give no variety, and presents a prodigious source in our gardens.

The *Coquelicot*, for instance, grows always the same in our wheat fields, and varies greatly in gardens; it is exceptional to find variations in the *Primeveres* of the fields, and there are few plants who furnish more when they are in flower beds.

The cause of the success which some florists have had with their seeds, is it not a result of what I just said, since nothing facilitates accidental variations more than the special care which certain inquisitive people take to mix their different kinds of tulips, *Oreilles d'Ours* and carnations? Their intention, in truth, is to please the eye, but they get without knowing it an advantage which they have often attributed to different infusions in which they may have set their seed to soak, to some colors which they may have mixed in the earth of their garden, to objects of different colors which they may have placed near their plants, or finally to good luck which

they may believe personal. I have tried the infusions and the mixing of colors, which have not succeeded at all for me, and I believe that there should be no need of experience to destroy the last two reasons.

Nothing is easier than to breed the huge numbers of varieties which may be born of these different mixtures: because when the dust from the stamens of red *Oreille d'Ours* should have made fertile a white *Oreille d'Ours*, the resulting seed should produce an *Oreille d'Ours* of which not only the petals will be streaked with red and white, but the embryos and dust of the stamens will share in one or the other. Then as a result this plant has no more need to be fertilized by another in order to make stripes, since it possesses in its own parts not only the disposition to make red and white, but still other different mixtures of the two colors which, combined one with the other, might make different kinds of shades which are very pleasant.

I might say the same thing of yellow, blue, and green, but I believe I have said enough to make it clear that the infinity of variations is no more extensive than can be that of the mixtures; and nothing is more in agreement than that, for example, which I have already reported, since two dogs of different species produce *Metis*, and these *Metis* produce others which give birth to a multitude of species almost without limits.

Always in pursuing this comparison one easily understands that the different organic arrangement of the participants (*parties*) may hinder the genera from mingling, and that if this should happen sometimes there would be born of them only a monster which could in no way reproduce its like, at least by seed. One understands equally that the disproportion in size and height in plants of the same genus may be an inconvenience in mixing species, just as is the difference in the time of their flowering, and deficience in neighboring plants; and it is to one of these causes that one can attribute the uniformity which one notices in certain genera, as in wheat, barley, oats, and other grains which give none or scarcely any variations; an observation which one can make equally about some kinds of animals, such as sheep, cattle, and almost all stock.

One notices that two plants which may seem to be much alike are found mixed together in the same field without uniting, while others which are in appearance quite unlike unite and give variations.

This is an exact imitation of what happens among animals, since there may seem to be much greater resemblance between a turkey-hen and a peacock than between a domestic hen and a pheasant. However, several people have assured me that the latter often takes a pheasant for her cock, and I am certain that the former does not take the peacock.

But I believe it is not necessary to confuse, with the variation of which I just spoke, certain monstrosities or diseases which several writers have meanwhile regarded as new species, such as plants with flat stalks, striped plants, and double flowers.

For I compare these kinds of accidents in plants to those faults which are hereditary and belonging to a whole family, such as a delicate chest or a blemish in the configuration of some limb, and I ascribe to them a similar origin, that is, some accident which happens ordinarily to animals like a fall, and so on, and to plants a hailstorm, a ray of sun, the puncture of an insect or even a too great abundance of sap which dilates the veins of a young plant, or a callus is formed, obstructions which deform it differently. But these accidents are scarcely my subject and might furnish material for another dissertation; it is enough for the present to have said a word to point out that it is not necessary to confuse them with the pleasing variations by which plants, without departing from the law which has been written for them, work at the multiplication of their kind and produce an inexhaustible source of good and pleasure. Perhaps these reflections may engage us to influence this mixture and this confusion in species of fruits, which growers observe, so as to produce for us by means of seeds an increased succession of new and excellent kinds of fruit.

Thomas Henchman

In the Autumn of 1729, the Reverend Mr. Henchman,[5] Prebendary of Salisbury, noted with surprise the spontaneous crossing of two varieties of "Pease" which had been planted side by side the previous spring. He was especially interested

[5] The Reverend Thomas Henchman was attached to Salisbury Cathedral as Prebendary of Gillingham Minor from 1717 until his death in 1746. He is buried in the Cathedral. There was also a Thomas Henchman who was Vicar of the Parish of St. Martin (1661) and of the Parish of St. Thomas (1667) both of Salisbury. If this is the same man he must have lived to be well over a hundred.

in the occurrence of different-colored peas in the same pod. On June 3, 1731, he wrote an account of his observations and sent it to Sir Joseph Ayloffe, who read it at a meeting of the Royal Society on July 1st. The paper was not published in the *Philosophical Transactions* and seems to have attracted no one's attention until Mr. Cromwell Mortimer (1745), Secretary of the Society, described it briefly in a footnote in Volume 43 of the *Transactions*. The footnote received little attention, although Charles Darwin knew of it and referred to it briefly (1868). The actual presentation of the paper is described in the *Journal Book* of the Royal Society. From Vol. 13, p. 635 (meeting July 1, 1731):

Sir Joseph Ayloffe shewed the Society two or three peas pods containing Heterogenous Seeds each pod having some peas white and some blew, and he communicated an account of their manner of production as he received it from the Rev'd Mr. Henchman Prebendary of Salisbury in a paper dated 3d June last. Who says that in the Spring 1729, a piece of his Ground being plowed up to be sowed with white peas and proving to be more than enough for the seed designated for it; One part of the remainder consisting of two double rows, was sowed with blew peas, and the other part being about four feet in width was left unsowed for a walk between the two plots of sowed ground. The event was that in flowering they mutually Impregnated each other so as to Generate white and blew peas within the same pod, sometimes more of one and sometimes more of the other according to the Specimens produced before the Society.

Sir Joseph had the thanks of the Society for this communication:

The *Register Book* of the Royal Society contains Mr. Henchman's letter (Vol. 16, p. 8).

Of the mixture of blew and white Peas in one Pod: communicated in a Letter to Joseph Ayloffe, Esq., by the Rev'd Mr. Henchman, Prebendary of Sarum: dated Sarum June 3rd 1731.

. . . . . .

In the Spring, 1729, I sowed a Piece of Ground for my Garden with white Peas; and my seed not holding out to sow all the Ground dug up, I sowed two double Rows of the Peas, with an alley four Feet wide between. In the Autumn, walking one evening between the Rows, I gather'd some for seed; and one of the shells opening in the gathering I was surpris'd to see one Blew Pea at the End next the Stalk, with six white Peas. I laid it carefully by, looking on it as strong Proof of Mr. Bradley's hypothesis of the Generation of Plants, which I was much pleased with from the first Reading of it, as very ingenious and highly probable, as I thought. But my curiosity did not lead me to enquire at that Time whether there were any more Shells with such a Mixture of the two Sorts of Peas in them.

In the Spring, 1730, as my Boy was rubbing out the Seed saved from that Plot to sow again, I observ'd a great many blew Peas among the White. Upon which I stop'd him, and took the Remainder, which I shell'd carefully myself one by one; and found great Variety of Intermixture of the white and blew Peas in the same shell: sometimes one white (or blew) only at one End, as in the first I took Notice of, sometimes at each end; sometimes two white (or blew) with one of the other colour interchangeably. I then laid by at least fifty Shells (several of each different Mixture) which I thought would be enough to satisfy the Curiosity of all my Friends, and fully establish Mr. Bradley's hypothesis. I kept them all the last Year, and this Spring gave several shells of them (of different mixtures) to Mr. James Harris Junior to carry up to London; and after that neglected the rest. I have still a few shells left; but they having lain unregarded in a window, the Sun hath scorch'd and forced them open.

Not having Plots of white and blew Peas standing near one another the last Year, I have not found any such mixture in the several Parcels of Seed then saved. In the beginning of this Spring I sow'd a Plot on purpose with a double Row of blew Peas on each outside of the Piece and all the middle Rows white. But the Weather prov'd so unkind at their first coming up, that it kill'd almost all of them. Yet I have two double Rows left (in a poor Condition) which I shall take Care to preserve for Seed; to see whether it will prove so upon a second Experiment, which I think there is no great Reason to doubt of.

And so the experiment came to an end. We must agree, however, with Mr. Mortimer, who ended his footnote reference by the comment: "But it is a pity he did not pick out a sufficient Number of blew Pease from among the White, and sow them by themselves, in order to see what colour'd pease this mix't Breed would have produced."

Apparently Mr. Mortimer's footnote was referred to in the article on Farina in the Supplement to *Chambers' Encyclopedia*, published in 1763:

The *Farina* of plants has been sometimes found to have an effect upon neighboring plants. Thus we read of russeting's changed by the *Farina* of a neighboring tree; and we have observations of pease of different colors infecting one another in like manner.

Jacob. Andr. Trembley

In 1734, Jacob. Andr. Trembley of Geneva published *Theses Physicae de Vegetatione et Generatione Plantarum*, a collection of thirty-six theses. This was done at the direction of Jean Louis Calandrini, under whose name the work is generally listed. Theses numbered from 22 to 27 describe sexual reproduction in plants, and those numbered 35 and 36 discuss plant hybridization. Obviously, Trembley made no experiments himself and his writings have no real value as scientific contributions. Nevertheless his paper illustrates very clearly the knowledge, beliefs, and standards of the early eighteenth-century biologists. From p. 10, Thesis 35:

Animals of different species having been mixed, a new kind of monster is born, the fœtus sharing in the form and nature of each parent; similarly, if the dust [pollen] of the stamens of any flower is carried by the aid either of the wind or of animals into the pistils of a flower of a different species, there arises fruit holding a middle course between the fruit of each parent: But this hybridizing is more miraculous in plants than in animals, for when, in the case of animals, an offspring has been born from such adultery, it remains sterile,

as if nature abhors these animals; on the other hand the monsters of seeds are fertile, and are able to multiply into an immense number of species; this happens because of the simplicity of the organs of generation in plants which clearly do not at all destroy the peculiar and suitable moistures, as happens in the case of animals.

Thesis 36:

It is more difficult to explain the nature of these plant monsters than it is to prove their existence by citing facts. The fœtus, enclosed from the beginning in the egg, imitates perfectly the nature and form of its own species; whence, therefore, this degeneration? The male by its own sperm supplies either the first rudiments of the fœtus or the first food for the tender fœtus in the egg, food, from which it is nourished and developed: but this is also the influence of the female, that the fœtus either arises from the female primarily, or at least it discovers new food in the uterus of the female and likewise a place for growing; why, therefore, is it marvelous if in the tender state of the fœtus, while it is growing and developing, its form and nature can be changed somewhat because of the natures of the father and mother? Not from any other source than this comes the communication of the diseases of the parents to posterity all too often observed. We are wisely silent concerning the other circumstances of the formation of the fœtus of an animal or plant. Already we are trying imprudently to reveal the very lofty and rather secret mysteries of nature; already, kindest readers, we have abused your patience more than is fair; it is time that we put a stop for the sake of the disgusted reader, for this reason at least, that we may repay your kindness by not abusing it any further.

John Mitchell

We do not know just when or where John Mitchell (d. 1768) was born. The first definite fact we have concerning him is that he studied under Charles Alston at the University of Edinburgh, where he probably received the degree of Doctor of Medicine. Sometime between 1721 and 1725 he migrated to Virginia, and in 1735 he became the Physician

to the Poor of Christ Church Parish, Middlesex County, Virginia. He lived in the little town of Urbana, and in 1738 he was made a Justice of the Peace. Eight years later he left America for England because of persistent ill health, and the next year (1747) he was elected a Fellow of the Royal Society.

During his stay in Virginia, he collected a great number of plants, corresponded with the leading botanists of Europe and sent numerous contributions to the *Philosophical Transactions*. The genus *Michella* commemorates this phase of his activity. His greatest work, however, was the famous *Map of the British and French Dominions in North America (1750)*.

Mitchell's contribution to plant genetics was first issued as *Dissertatio brevis de principiis botanicorum et zoologicorum (Acta Phys. Med. Acad. Leopaldina . . . Ephemerides)* 8: Append. 178-202: 1748; later it was printed separately (Norimbergae, 1769). This essay was first sent to Peter Collinson, who in turn submitted it to the *Ephemerides*, where it was published just ten years after it was written. The work was really composed while Mitchell was living in Virginia, for it is dated as follows:

Dabham ex aedibus meis
Virginia 1738

Mitchell himself made no original observations, indeed it it possible that he never saw a plant hybrid. He understood the significance of hybridization, however, and he made a most logical attempt to place taxonomy on a genetic basis. If his suggestions had been followed it is possible that today we should have neither "splitters" nor "lumpers." At least the species concept would be precise and classifications would be on an objective basis.

Mitchell's dissertation is divided into thirteen sections; sections numbered 7, 8, 9, and 10 deal with animal, and

sections 11, 12 and 13 with plant hybridization. The following translation (Nos. 10, 11, 12, and 13) is not literal.

10. According to this same principle it is definitely agreed concerning the coming together of different species of animals. For whenever two individuals produce fertile and prolific offspring we must admit that they differ only in their nonessential qualities and but little in their specific characteristics. I find that the celebrated John Ray agrees with this belief of mine. Ray, a most fair judge of Botany and Zoölogy, has written in his tract concerning creation. "I reckon all dogs to be one species, they mingling together in generation and the breed of such mixtures being prolific." Thus, if we derive very sure evidences of the *specific* similarity and dissimilarity from an animal, why should we not also seek the *generic* similarity and dissimilarity from a like source? For since we see so much diversity in the progeny of animals of different genera, is it not abundantly clear that this production belongs in a different category in the chain of nature? Besides, since we see many animals propagating and maintaining their species, however dissimilar they may be in some nonessential qualities, we must consider them related not closely but by *specific* characteristics. And again, those who are able to produce offspring by cross breeding, no matter how sterile it may be, are joined by the next degree of relationship; they belong to the same genus. While, on the contrary, those who can produce no offspring of this type or else a different kind of offspring, have a different degree of relationship and are not of the same genus. Because of the differences in their structures and natural organs, animals of different genera are essentially adapted for different functions. But whether I can go further here and pronounce those ὁμόφυλος to be of the same tribe who produce a hybrid offspring and to be of different tribes if they can produce only a monster or no progeny at all, I am unwilling to decide without experiments, lest I seem to favor my own conjectures too much, even though they are essentially reasonable. This assumes, of course, that the production of these creatures is natural and constant, which I have not seen demonstrated. According to these principles I believe that the *species* of animals will have to be somewhat narrowed; but how far this should go experiments will have to show.

Thus *Dana Virginiana* seems to me to differ least from the animals of the common European species, however much it may differ from the deer in its beautiful and elegant body form, in agility and smoothness and in the branching of its horns; I also believe that the same is true of the gray fox, the small red hare, the small partridge, our gray and red squirrels, our native and the common Canadian beavers, and many other American animals. I merely mention these in passing.

11. Now for a few things concerning plants to follow this discussion of animals; plants are entirely similar, they have the same chains of relationships and delight in the same method of generation [as animals] according to the doctrine of Moreland, which has later been approved by Geoffroy, Miller, Bradley, Logan, and others from whose observations I shall adopt the following postulates which I hope to demonstrate (and if I do not surely demonstrate them beyond a reasonable doubt, I beg the botanists to assist me in examining and clarifying the matter still further). Postulates, (1) Plants with masculine and feminine organs of generation use them in the same manner as animals; (2) plants which everyone recognizes as belonging to the same species are mutually cross fertile and produce prolific offspring. Miller proved this satisfactorily in cabbages (*Phil. Trans.* 1721) and in many other plants, particularly in the garden plants which we see every day. So why does not this hold true concerning those species where at present there is some doubt? Surely we see that nature is always simliar to itself in similar things. And so if the innumerable variety of plants, now causing work for the botanists, often, if not always, arise from cross fertilization, I ask what clearer evidence or more certain sign that these *are* varieties can be desired than this power of cross impregnation proven by sure experiments? (3) Plants, of different species but which no one doubts belong to the same genus because of their resemblance in many primary attributes, cross fertilize each other but produce a mule-plant which cannot propagate the species. Probably the relationship of animals to plants is shown by this mule, which Bradley described [see page 111] as descended from the carnation and sweet william. It seems to me that to this type of mule belongs the *Hyacinth Sannisius*, that monster of nature concerning which there are so many doubts. And so if the carnations and pinks or any other plants cross fertilize each other

it is certain that all plants as closely related or of the same genus may produce an offspring of the same kind, for nature is uniform in all things, and if those of the same genus produce mule-plants, why must not those which produce either a hybrid or no offspring at all be considered as differing in genera? For, as I have said above concerning animals, if those plants which produce prolific fertile embryos are alike in species, surely those which produce on cross fertilization progeny of an almost similar type to these must belong to the same genus, nature having united them in the next degree of blood relationship, while those which produce only hybrids (provided they are such by an unchangeable law of nature) are related in the next degree in nature that is in the same tribe or family: but nature sets other forms further apart which are unable to procreate or which can produce only monsters.

12. Thus it seems to me from the above that the generic relationships of plants may be discovered by [breeding] experiments, and I scarcely think that the learned botanists are unaware of the manner of making these experiments or of the precautions which are necessary; if the stamens and apices of one plant are cut out before the fertilizing dust is mature and before any of it is shed, and if the stigma of the castrated plant is lightly sprinkled with the fertilizing dust of another plant as often as may be necessary, and if this crossing produces fertile and prolific seed in turn, then the plants belong to the same species; but if the seed produced from the cross, no matter how active and fertile it may be, grows to be a plant which is unable to reproduce itself, or if it grows into a mule-plant, the parent plants which were crossed belong to different species but the same genus: if no offspring or a hybrid offspring is produced the parent plants belong to different genera.

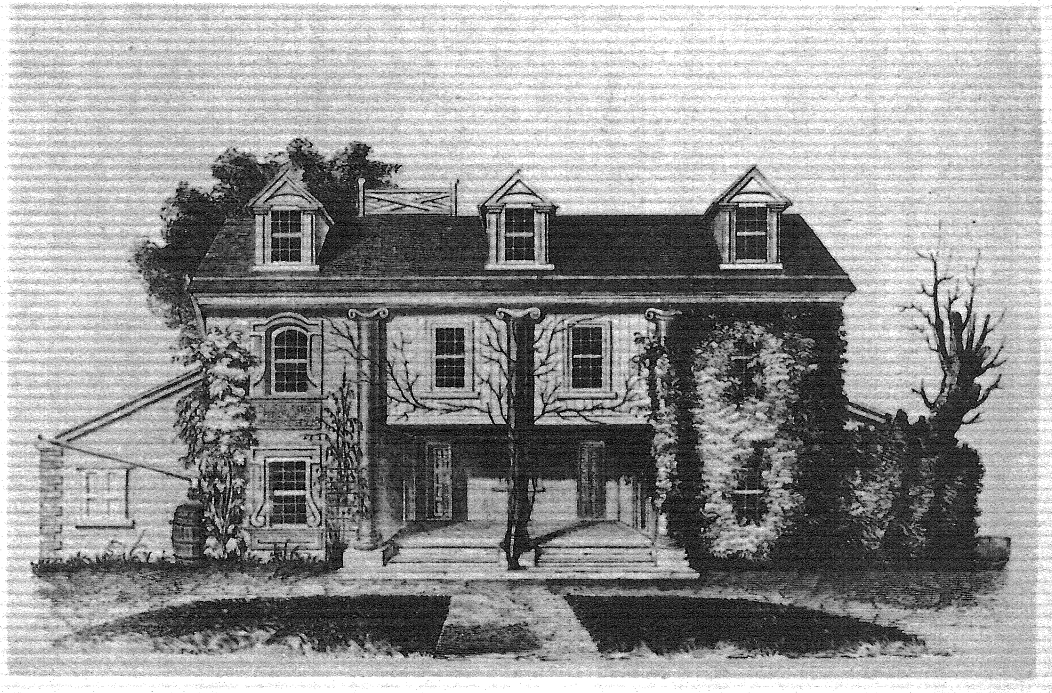
13. Genera having been defined in this manner, which is indeed a fundamental principle for botany, a further basis is demanded for determining the association of plants into classes and orders, or into tribes and families. It is evident, according to my hypothesis, what must be learned. Nature herself may in this manner decide, but the botanists' [conclusions] seem to be doubtful and contrary to experience, since, at least until the present, the classes, with one or two exceptions, seem to have been derived from the minds of the botanists

rather than from the ways of nature. Although this classification is highly necessary for teaching, the artificial division and connection of these categories does oppose both the laws of nature and those very genera and species which are the work of nature herself.

John Bartram

John Bartram (1699-1777) is best known as a collector of American plants who made several expeditions beyond the frontiers in search of new species. He lived near Philadelphia and collected and exported plants at a time when European botanists were most anxious for specimens of the American flora. For thirty-five years he corresponded regularly with the celebrated Peter Collinson, and during this period he sent an enormous number of seeds, roots, and dried specimens to Europe, perhaps more than any other American botanist. He received in exchange many exotic species, and the botanic garden he established near Philadelphia was the first one in America to contain both native and foreign plants. He was in communication, also, with many of the leading botanists of the world, and today his published letters are a valuable source for the study of much of the early development of science in the Colonies. He corresponded with Sir Hans Sloane, Dillenius, Catesby, Fothergill, Gronovius, Linnæus, Philip Miller, and many other scientists and his very real ability seems to have been recognized and appreciated.

Bartram began his study of botany as a protégé of Governor Logan. Sponsored by Logan, he was soon an intimate friend of many of the Colonial leaders—Benjamin Franklin, William Byrd, Dr. Colden, and others whom he met on his travels. In 1738 he traveled throughout Virginia in order to find new botanical specimens, and by 1751 he had explored western Pennsylvania and northern New York. In 1760 he visited the Carolinas. Five years later he traversed tidewater Georgia and ascended to the head waters of St. John's River



BARTRAM'S RESIDENCE

Built with His Own Hands

in Florida. It was at this time that he was appointed Botanist to the King, receiving for his duties a small royal pension. In spite of the fact that his formal education was limited, his interests were extensive and he kept in close touch with all of the contemporary developments in his favorite science. At no time during the period of his botanical activities was he interested merely in the collection of new forms. He observed carefully the native habitats of the different species, he studied their soil requirements and their seed production, and he was one of the first in America to produce hybrid plants.

Our records of Bartram's experiments in hybridization are very incomplete. We have indications that he described his work in three letters, only one of which still exists, i.e., the letter written to William Byrd in 1739. It is probable that another letter written to Peter Collinson on April 29, 1740, also contained an account of the hybridization, but this letter is now lost. Collinson's answer, however (July 23, 1740), indicates that Bartram had described his hybrid. The existence of the third letter is more problematic. In his letter to Byrd, Bartram stated that his experiments were "to oblige some ingenious botanists in Leyden," and as he was at this time in communication with Gronovius, it is only reasonable to suppose that he sent the latter an account of the experiment. An undated manuscript in Bartram's handwriting describes a species cross in *Lychnis*.

Bartram's letter to Byrd was published by Darlington in 1849. Although Darlington had been a member of Congress for six years, he remained a man of the most delicate sensibilities, so delicate, in fact, that he omitted from Bartram's letter just those portions which describe the sexual parts of flowers and the hybridization. The letter, or probably the copy of the letter which Bartram kept, is now in the files of the Pennsylvania Historical Society, and we are not depen-

dent upon Darlington's bowdlerized version. The letter is not dated, but it mentions Byrd's letter "by ye post last winter; and another dated March ye 23d, which I received by ye hand of thy friend doctor Tschiffely." As both of Byrd's letters still exist, we know that Bartram's letter was written in the year 1739.

John Bartram to Col. Wm. Byrd
(Bartram Papers, Vol. I, fol. 19)

Dear Friend Coll Byrd:

I r'ceived thy kind letter by ye post last winter; and another dated March ye 23d, which I received by ye hand of thy friend doctor Tschiffely, whom I recieved very kindly and made as welcome as my present Circumstances would afford for thy sake having no other acquaintance than thine and another[6] recommendation. I have this spring made several microscopical observations upon ye malle and femall parts in vegetables to oblige some ingenious botanists in Leyden, who requested that favour of mee which I hope I have performed to their satisfaction and as a mechanical demonstration of ye certainty of this hypothesis of ye different sex in all plants that hath come under my notice. I can't find that any vegetable hath power to produce perfect seed able to propagate without ye conjunction of malle seed any more than animals and by a good microscope ye malle and femall organs is as plainly discovered. I have made several Successful experiments of joyning several species of ye same genus whereby I have obtained curious mixed Colours in flowers never known before but this requires an accurate observation and judgment to know ye precise time when ye femall organs is disposed to receive ye masculin seed and likewise when it is by ye masculin organs fully perfected for ejection. I hope by these practical observations to open a gate into a very large field of experimental knowledge which if judiciously improved may be a considerable addition to ye beauty of ye florists garden.

A part of the letter from Peter Collinson to John Bartram has also been published by Darlington (1849).

[6] Isham Randolph also gave Dr. Tschiffely a letter of introduction to Bartram. This letter is dated May 24, 1739.

Peter Collinson to John Bartram
(Bartram Papers, Vol. II, fol. 53)
London, July 23d, 1740.

Dear Friend:

I had the pleasure of thine, of April 29th, 1740. Thy experiment of the usefulness of the *Farina*, is very curious and entertaining, where plants of a class are growing near together, they will mix and produce a mingled species. An instance we have in our gardens, raised by the late THOMAS FAIRCHILD, who had a plant from seed, that was compounded of the Carnation and Sweet William. It has the leaves of the first, and its flowers double like the Carnation—the size of a Pink—but in clusters like the Sweet William. It is named a *Mule*—per analogy to the mule produced from the Horse and Ass.

Writing on these matters, brings to mind the Papaw—an Indian fruit—which in our stoves is produced in great plenty. On this tree, is very remarkably distinct, male, female, and hermaphrodite blossoms, which are very extraordinary to see: but whether the last is an assistant in generation, or is a sport in nature, is not yet agreed. . . .

Dr. WITT's hollow-leafed Lavender, is no doubt, the Side-saddle flower; but what relation it has to Lavender, I must leave to him. The plant with tricolor leaves, I am well assured, is your fine *Clinopodium*. Our late severe winter has carried all mine off; so pray send me some more seed—and of the *Lychnis* with Crosswort leaves. . . . The Flesh Colour[7] *Lychnis* does not appear but in its Roome One with a pale Blew Flower perhaps this may be that from Susquehannah a new one and very sweet sented which I esteeme much—and I want when thee increases it, that with a white flower with a Red Spott in the Center, and that *Lychnis* with a small white flower. . . .

What curious experiments did Bartram recount in his letter of April 29, 1740, which caused Collinson to comment, "When plants of a class are growing near together, they will mix and produce a mingled species," and to follow the comment by a description of the then twenty-three-year-old hy-

[7] Not skin-color. In 1740 "flesh-colour" meant light red, like the "meat" of the watermelon. All of these plants may not have belonged to the genus Lychnis as now understood; at least the blue one was a species of Phlox.

bridization experiment of Thomas Fairchild? The inference is obvious; i.e., that Bartram described his own work on species crossing. The mention of the flesh-colored Lychnis also serves to connect this reply of Collinson's to Bartram's hybridization. It would seem that Bartram intended to send this flower to Collinson and, through some mistake, another arrived in its place. The flesh-colored Lychnis was Bartram's hybrid.

The following is transcribed from an undated MS in Bartram's handwriting which is now in the possession of the Pennsylvania Historical Society (Bartram Papers, Vol. I, fol. 20). The MS, consisting of a frayed sheet of paper with a large fragment torn from a corner, shows signs of being very hastily written; i.e., words inserted between the lines, words duplicated, letters small and less clearly formed than usual. The paper had been torn before Bartram wrote on it, so it seems improbable that he ever intended to include it in a letter. The MS has the appearance rather of a preliminary draft, possibly of the missing letter to Collinson.

. . . have had for 3 year a lychnis which produced flesh-coloured flowers male female upon several plants, one large plant which produced malle over most part of summer but produced no seed which engaged my particular notice and I observed that that seed was produced which ye sent me distinct male and female plants a year after I had sent from eng[land] some of ye seed of white lichnis which produced male & female flowers distinct upon different plants. It happened that one female plant flowered near two weeks before any male flowered which I obsrved daly and observed that tho there was no stamina or anthera in ye flower yet ye capsula was filled with perfect seed which I sowed as soon as it was ripe which came up very well in a few days but by that time ye capsula of this first flowering white lychnis was near full grown then several malle plants flowered in the same bed. I then puled of all ye capsulas that was set before any of these male flowers of ye white lic[hnis] appeared & that which was produced after ye male blossoms opened and shed

their farina: for I concluded that either that this female white lychnis must be impregnated with ye male red lychnis which grewed 10 yards of it so then it must pertake of ye nature & ye color of ye red one or else we should be pusled to reconcile ye hypothesis of necesity of ye male & female parts as after it had happened according to my expectation for it produced flowers a great deal paler than y red & as ye seed of ye white lychnis that was produced after ye male plant flowered produced plants which bore flowers as white as their original. Morover I gave docr witt one plant of ye female lychnic which flowered plentifully with him & produced ye capsula but containing onely something like ye husks of ye seed but no vegitive life on them, by which it appears that ye male parts of vegitables is really as necessary to vegitation.

Daniel Rudberg

With Rudberg we come to the first of Linnæus' students who discussed the problem of species crossing in plants and who listed instances of plant hybridization. It is difficult, if not impossible, to decide how much of the work represents the efforts of the student and how much of it is really Linnæus at second hand. Sachs unhesitatingly ascribes it to the latter, but Sachs was hardly a fair judge in matters concerning Linnæus. There is corroboratory evidence, however, that these dissertations, which were later collected and published in the *Amœnitates Academica*, are really the work of Linnæus. Haartman, who wrote one himself, refers to this dissertation of Rudberg's on *Peloria* as the work of Linnæus. On the other hand, Linnæus is always cited in the third person, sometimes as "our President," and sometimes as "our noble" or "our famous President." Moreover, he is given such fulsome praise throughout these essays that it hardly seems possible that he was humorless or vain enough to write them himself, even though he was an eighteenth-century scientist. Thus, no decision can be reached on this point at present.

Daniel Rudberg's dissertation, *Peloria*, appeared under the

date of December 19, 1744, and it was printed in the *Amœn. Acad., Vol. I.* In this paper he describes a number of varieties of Peloria in detail. He assumes that the genus itself is of hybrid origin, and he discusses the general question of plant hybridization. The following lengthy quotation represents the major portion of his contribution to this topic.

From *Amœn. Acad.*, I:

It has hitherto escaped us just what the cause of the change of the Linaria into the Peloria might be. When some such thing happens in the animal kingdom, it must be attributed to the unnatural marital union of two species whence is born a certain intermediate product, which is a mixture of both, examples of which are seen in mules and a few other animals. But these hybrids are not propagated, for nature forbids it, lest there be more species of quadrupeds than there were in the beginning. Thus, the *Passer Canariensis,* wedded to the *Acanthus femina* produces offspring which are fertile in the first generation, but all the grandchildren are sterile. In the vegetable kingdom, as far as the odor, taste, color of plants are concerned, varieties are often detected. Experiment shows this in the case of tulips, for when its flowers are fertilized by flowers of another color, the seeds generated from these treated flowers bring forth blooms of different colors. Likewise, the pure white variety of the *Brassica* often produce seeds which in turn produce the sky-blue vulgar *Brassica,* and this happens if the first is growing in the neighborhood of the second when they are both in flower.

Moreover, it is a fact that different species have been bred in the vegetable kingdom of which few, or rather no, traces of antecedent times has experimentation laid bare. Nor can we perceive otherwise but that the Peloria came into existence by a fertilization of this sort. If the location, climate, or nourishment had effected this change, then on the same stalk we would see flowers, some more, some less, in accord with the structure of the Linaria. But this is not the case. For in all the individual flowers of the Peloria, so exact a peculiar likeness has been discovered that not even the larger one of the flowers of the Linaria has appeared. However, we confess that we do not know by what other flower the Linaria has been impregnated when it produces

the Peloria, and this has been the final pronouncement of one who has observed the plants which bloom at the same time and in the same place as the Linaria. Besides it must be noted that in the flowers of the Linaria the neck is almost closed so that it would be very hard for it to admit the pollen of some other flower to fertilize its pistil unless the lips of the corolla had been torn and eaten away beforehand by insects. It seems on first sight a paradox that new species, nay, even new genera, should arise from the copulation of different species in the vegetable kingdom; meanwhile observations persuade us that this very thing takes place. Why all the cacti in America? Why so many species of aloes and geranium at the Cape of Good Hope? The *Saxifraga,* with the lineate petals, as if from the *Parnassia* and the *Saxifraga,* the *Hyoscyamus,* as if from the sire *Physalis* and the mother *Hyoscyamus.* The *Primula* with the cordate leaves, as from a sire *Cortusa* and the mother *Primula of the Auricula ursi. Tragopogon,* perhaps from a father *Papsama Bhagadiolus* and a mother *Iragopogus purpureus-caeruleus.* The *Poterium Agrimonodes* apparently from the sire *Agrimonia* and the mother *Sanguisorba.* The *Datisca* apparently from a father *Cannabis* and a mother *Reseda Luteola:* this conclusion is made with ease upon comparing the flowers. Numerous varieties of many species are being inspected attentively. Observation and time will determine how certain these theories are; I propose them not as proved, but merely problematically, that others may inquire more accurately into this subject.

Following this paragraph, Rudberg printed an excerpt from a letter written by Johann Georg Gmelin, who stated that new varieties of Delphinium, which appeared spontaneously, could best be explained by the assumption that their maternal parents had been fertilized by foreign pollen. Rudberg then attempted to interpret Marchant's observation on Mercurialis:

In the *Actis Paris* in 1719 Master Marchant exhibited a plant produced in his own garden in July, 1715, unknown to himself and other Botanists as well, which remain intact up to the end of December, and which he called the *Mercurialis foliis capillaceis,* since it could be

properly referred to the genus *Mercurialis*. In the following year, in the month of April, six other plants were born in the same place, four of which seemed like that prior one, but the other two were still different, so that he decided that they were a new species and called it *Mercurialis foliis in varias et inaequales lacinias quasi dilaceratis*. Master Marchant disputed a great deal in the *Act. Paris.* about the method in which these had been produced. Seeing that the plant was agglutinated, our President[8] recognized that this was identical with the *Mercurialis caule brachiatu, foliis glabris,* in flower, odor, stem, etc., except that its leaves were incised, which variety is not infrequent in the vegetable kingdom, and can be the result of a diversity of soil in its natal place, a fact observed in the *Pimpinella* and other plants.

If it can be decided with certainty that the Peloria must have arisen as a hybrid species from the *Linaria* and some other plant, a new truth would come to light in the vegetable kingdom, and that process [i.e., hybridization] in the case of plants would be further advanced than in the case of animals in that animal hybrids, like Mules and others, lack the ability to propagate themselves. But we see that the Peloria propagates, for it has perfect seeds and in its natal place multiplies copiously and of its own accord. But future experimentation must investigate whether a *Linaria* is ever born from the seeds of the *Peloria*. But if, as seems probable from observations now made, this does not happen, but the Peloria remains constant, thence follows a mighty thesis; it would become an undoubted fact that new species make their appearance in the vegetable kingdom; that the genera may exhibit differences in fructification, but rejoice in one and the same nature and strength; nay even, that one and the same genus may have diverse fructifications. By this thesis the fundamental principles governing fructification, which is the foundation of the whole science of Botany, would be destroyed, and it would infringe upon the natural classes of plants, to such an extent indeed that in our *Peloria* all who are skilled in our field would wonder, not without reason, at the stupendous fruit of Nature.

Rudberg concludes as to the origin of *Peloria:*

By asserting that Peloria is derived from and produced by Linaria, we will seem to affirm something at first astonishing and incredible,

[8] Linnæus.

but scarcely unwarranted. Nor is it a greater miracle for Pyrus to produce Narcissus, or Carduus a fig tree, or Spina [?] grapes. Nevertheless, there are so many and such great considerations, which demonstrate with certainty that *Peloria* is generated from *Linaria*, that no one, seeing both plants and instructed by a comparison of them, could deny it.

This paper of Rudberg's attracted the attention of a number of contemporary botanists. Both Gmelin (1749) and Gessner (1753) quoted from it extensively. The paper, *De Floribus Peloriae nascentibus in Elatione foliis subrolundis* published by Johannes Rodolphus Stehelin in 1752 (*Acta Helvetica* 2: 25-33) is especially worthy of attention as the author described and pictured a flower of *Peloria* upon a plant of *Linaria*. He interpreted the occurrence as a case of degeneration. B. Sprenger (*Opuscula physico-mathematica*, Hanover, 1753) stated, "The *Linaria* frequently generates with wild forms. The broader mouth of the *Linaria* remains forever in the mixed family."

Johann Georg Gmelin

Gmelin[9] (1709-1755) is remembered chiefly for his *Flora Siberica*, St. Petersburg, 1749-50, a book which describes the

[9] In the article on "Hybridism" by P. C. Mitchel, in the eleventh edition of *Encyclopedia Britannica*, occurs the following interesting and probably erroneous statement: "The earliest recorded observation of a hybrid plant is by J. G. Gmelin toward the end of the seventeenth century; the next is that of Thomas Fairchild, etc." Now obviously Gmelin was relatively quiescent in the seventeenth century. His father, however, was also named J. G. Gmelin (1674-1728) but Pritzel records no publications of the latter and in the *Allgemeine Deutsche Biographie* it is expressly stated that he did not publish. It is probable that Mitchel was simply careless in his condensation of the article on Hybridism by Romanes in the ninth edition of the *Encyclopedia*. Romanes stated, "The knowledge [of hybridization] . . . in the vegetable kingdom necessarily dates from a time subsequent to that at which the sexual function of plants became known, i.e., toward the end of the 17th century. The earliest recorded observation of a hybrid plant is one by Gmelin: the next is that of Thomas Fairchild who, in the second decade of the 18th century, produced . . . Fairchild's Sweet William." Strangely enough both Romanes and Mitchel date Gmelin's work before Fairchild's, although he was only eight years old when the first record of Fairchild's hybrid was published. This misunderstanding could have arisen by a careless reading of Focke's *Pflanzenmischlinge* (1881). Focke cited Gmelin's work before Fairchilds but without giving it a date.

plants he found in his exploration of Northern Asia. He spent the years between 1733 and 1743 in that inhospitable region, collecting the plants and seeds which he later introduced into Europe.

Two species of *Delphinium* were among the new plants which he brought back from the east. These he planted in his garden and shortly thereafter found to his surprise that they had produced five or six different varieties. He ascribed this production of new forms to cross pollination, and he communicated this view on May 17, 1745, to Wahlbom, who had just published a similar interpretation of the origin of *Peloria*. Wahlbom included a part of this letter in the edition of his paper which was printed in Vol. I of the *Amoen. Acad.* This excerpt follows:

I have seen in the *novella Holmensia* that you published an article on the *Peloria* and I cannot refrain from telling you that the idea entered my head over a year ago that new plants are made occasionally from the copulation of different species or genera, just as in the animal kingdom the Mule is born from the Ass and a Mare. And as this happens but rarely in the animal kingdom, even so it may not happen often in the vegetable kingdom. In my rock garden I now possess five or six *Delphinia*, the differentia of which I can indicate, but I brought only two species from Siberia. Certainly there are many difficulties in the science of Botany still to be explained which can be explained by this theory if we adopt it.

Gmelin later published the same explanation in the *Flora Siberica*. In describing *Delphinium* he wrote (From Vol. IV, p. 188, Edition of 1769):

This wonderful plant has so many varieties that to recount all of them would be tedious. Neither the great length of the leaves, nor their smoothness and hairiness, nor the deep or shallow incisings of the leaves, nor the different sizes of the flowers, nor the subrotund or oblong shape of the petals are of any avail in determining the peculiar species of this plant. For this plant occurs very promiscuously in

its natal place and it has the habit of varying more and more when transplanted into gardens; the lappets of the leaves are often so narrow that they correspond completely to the lappets of the first species, and the first species has often such broad ones that they vary but little from the width of those in the second species. Thus, the garden varieties show what our explorers have never observed in the woodland varieties. I observe as others have noted, also, that when these plants are grown on their native soil, one species is rarely adjacent to another, since one is a native of dry, sunny fields, while the other species, about which we are talking, takes more delight in the woods, plains, and the wooded banks of rivers and streams. Whether or not the close proximity of the two species has brought about the mutual commingling of the seeds, no change has been made in the flower or fruit, but only the leaves have undergone a change. In Russia it is called ПРИКРИМЪ and it grows throughout Siberia to Kamchatka.

Gmelin's longest discussion of plant hybrids was published in his *Sermo academicus de novorum vegetabilium post creationes divinam exortu.* Accedit Rudolphi Jacobi Camerarii *de sexu plantarum epistola,* Tuebingae, 1749. Here he described the sexual reproduction of plants and the origin of new species through hybridization. He summarized the work of Camerius, Logan, Linnæus, Swammerdam, Reaumur, Ray, Willughby, and others and quoted at some length the work of Wahlbom on *Peloria.* The following extract is taken from pages 77-82. In regard to *Peloria,* he stated:

He [Linnæus] should not have been in doubt about this because such plants have already been seen in Germany and because a flower of the same class such as the *Elatine,* has been transformed in a like manner. As if, to be sure, illicit love affairs did not occur in Germany! The species of the mother, *Linaria,* is born in great profusion in Germany, but doubt as to the father cannot be removed until it is determined what type was in Sweden. And so, the conjecture of the celebrated Linnæus is very near the truth, and in this he will certainly receive indulgence from all, from even the more peevish botanists, because Linnæus reasoned most carefully and secured his evidence

through actual observation. He wishes to introduce hybrid species into botany. But they will judge him less kindly when he attributes to hybrids the ability of propagating themselves. His *Peloria* has matured seed, and in its place of origin is multiplied spontaneously and plentifully; from which he rightly judges that *Peloria* will remain a constant species. Further observations will show whether seed continues to be set (for this cannot be decided by a mere inspection) and if this seed will, after many generations, never produce any plant other than *Peloria*, no doubt will remain that new plants appear from time to time as new creations of a Divine Creator. At least they multiply in such a way that they seem to have been created originally after the fashion of other plants. I do not believe that there is anything contrary to Divine Majesty in this because the origin of a plant of this [hybrid] type is secured by the use of those organs which God created in plants, and consequently this ability to produce new species from old can be considered a lawful method of propagation. But I doubt if the question can be settled from this one example, in such a manner that fear of its not being true may not occasionally arise. Indeed there are many plants numbered by the ancients of which we have no knowledge today, and I suspect this fact is due to the following: A hybrid species, having replaced the parental types, exists [for a time] and disappears little by little until it [in turn] is replaced by the parental species. The present-day activity of botanists, however, has rediscovered a number of species which had been abandoned, and this raised the hope that other species still sought will ultimately be brought to light. From the fact that more species of plants have been collected in modern times, the celebrated Linnæus tried to prove, by examining the external structures of the flowers, that hybrids had been produced from the earlier species by cross breeding, and he even added to this proof by making a new product which he prepared from *Peloria*, but whether he reached his objective in any way whatever, only time, observation, and experiments will tell. Without these all of our judgments concerning nature are mutilated and defective. Because he believes that the herb henbane originated through pots of the common henbane having been blown into from *Physalia*, he would rejoice if *Physalia* were ever found in Siberia, because its occurrence there would increase the probability of this origin. In order that we may accept the above

we must assume that the seeds of *Physalia* had blown from Spain, Mexico, Malabar, Curaçao, or from an island in the Danube or from Italy or Germany to the waterfalls of the river Angara, the only habitat of this herb henbane known at present, and that these seeds had produced plants similar to *Physalia*, whose anthers produced dust which impregnated the common herb henbane, the *Physalia* afterwards disappearing. To be sure these suppositions are somewhat excessive and ought to be investigated a little further.

Concerning the *Dracocephalus floribus vesticillatis, bracteis oblongi, integerrimis, corollis vix calicem superantibus*, Linnæus in *Horto. Upsal.* p. 167, n. 7, makes the same rather probable conjecture, i.e., of its hybrid origin. For the corolla in this plant is like the *Thymus* but the calyx resembles exactly the calyx of the *Dracocephalis floribus vesticcillatis, bracteis oblongis, ovatis intergerrimis, corollis calice multatis majoribus* Ups. lc. m. 6. But both these plants, the *Thymus* and the *Dracocephalis* with its larger corollas are born in places not so far apart but that they are perhaps able to cross breed so that there is an opportunity for the production of hybrid plants, if distance alone hinders the formation of hybrids, because the whole region from the point where the Irtish river turns eastward abounds with both *Dracocephalis corollis calice multatis majoribus* and *Thymus* in absolutely equal abundance which it also does in regions situated west of the Irtish; but in more eastern regions the *Dracocephalis corollis calicem vix superantibus* never appears. Are these eastern plants then purer than the western?

In the same book (p. 249) concerning the *Carduo tormentoso pyrenaico, floribus purpureis glomeratis*, Tournfort I. R. H. 441 (the thing having been without doubt observed accurately), Linnæus affirms that this plant appeared yearly in the garden at Upsala from the seed of the *Carduo eriocephali degeneris*, and it is not known whether it sprang from the seed of the *radii* or the *disci* or whether from a hybrid copulation. I myself suggested to the celebrated Linnæus the example of *Delphiniis Sibericis*, of which I observed in Siberia never more than two species. But in the garden I tended in Petropolis, I counted up to five or six species. . . . The difference between most of the varieties was in the leaves, i.e., finely or coarsely divided, darker or lighter in color, stronger or delicate, upright or pendant, with more

flowers or less. Often, however, the differences were of a kind which kept the observer in doubt as to which species the plant should be assigned. I believe, from the preceding statements, that this variability was caused by the pollen of one species falling into the stigma of the other, whose anthers had not yet performed their duty. I can conjecture this the more because these two species, which nature truly had separated, had been planted in the same neighborhood.

Gmelin next printed a letter he had received from Linnæus, and closed the essay as follows:

And so, doubtful observations and arguments having been here repeated, certain conjectures are held and seem quite probable, that hybrid species occur in the vegetable kingdom and that this illegitimate birth does not affect the characters of the leaves very much, but only those parts devoted to the formation of the flowers and the fruits. It is unknown, though, how many generations hybrid species of this type are able to continue. Therefore some plants at least escape notice as new and distinct species which have arisen after the Divine Creation. Observations upon the animal kingdom do not very strongly oppose this view in so far as it pertains to the manner of procreation; if only you make exception of the duration of the hybrid species, which in animals does not yet continue for many generations because of their lack of fertility. Careful observations continued through a series of many years, and experiments cautiously and skilfully set up, will lead up at last to complete truth, for accomplishing which all our strength must shine forth.

Benjamin Cooke

Benjamin Cooke, F.R.S., lived at Newport in the Isle of Wight. He was a cousin of Peter Collinson and, like Collinson, interested in things botanical. Some of his communications to Collinson were later sent to Sir Hans Sloane, while others were published in the *Philosophical Transactions*. Cooke's observations of hybridization were enthusiastic rather than critical, yet he did observe the crossing of color varieties of *Zea Mays*. His description of the corn silks blushing as a result of their commerce with an alien pollen is fanciful, to say the least, and we should perhaps interpret his hybrid ap-

ples as bud sports. On the other hand, he made real attempts to hybridize plants, and correctly interpreted the mixture of different-colored grains in the ears of corn.

The following letters are reprinted from the *Philosophical Transactions*. Vol. 43, pp. 525-526.

Extract of a letter from Mr. Benj. Cooke, *F.R.S.*, to Mr. Peter Collinson, *F.R.S., concerning the Effect which the* Farina *of the Blossoms of different Sorts of* Apple-trees *had on the Fruit of a Neighboring Tree.*

Newport (Isle of Wight), *Oct.* 1745.

Dear Cousin,

I have sent you some Russetings changed by the Farina of a next-door Neighbor, whose Name I wanted Skill to know; but can only say, that the *Russeting* has exactly acquired his Face and Complexion.

(*Mr. Collinson* then produced several Samples of the Apples; an unteinted Russeting; a Russeting changed in Complexion, which grew among a great cluster of unalter'd Brethren; and some Apples of the other Tree, which had caused the Change in the Russetings, and whose Fruit had in Return received a rough Coat from the Russetings).

Theophrastus takes notice of this παραλλαγη as he calls it; and tells us the old Divines were wont to make great bother about it, and foretel great Events by it; Pliny informs us, there was one who wrote a whole Book about such Changes. But the Use I should make of it, is chiefly this, that it may be of Importance to the Curious in Fruits, to take care how their Trees are sorted, and what Company they keep. For tho' this Change be not so conspicuous in Apples which have a smooth green Coat, as in the Russet-breed, yet one may suppose Impressions of this sort often made on them; and perhaps their Juices alter'd for the better or worse.

Yours, &c

B. Cooke[10]

The Apples shewn
Nov. 14, 1745.

[10] This letter was translated into German and published in the *Hamburgisches Magazin* 2:120-122 (1747). George Friedrich Möller did not like it at all and attacked both Cooke's conclusions and the general idea that plants reproduced sexually (*Hamb.*

Vol. 45, p. 602.

IV. *A Letter from* Benj. Cooke, *F.R.S., to* Peter Collinson, *F.R.S., concerning a* mixed Breed *of* Apples, *from the Mixture of the* Farina.

Newport, Dec. 4, 1748.

Dear Cousin,

I sent you last Year a Specimen of the Effect of the *Farina* of a rough-coat Apple striking on the Flower of a smooth coat; I have now sent an Example of the Farina of the Latter changing the former into its own Dress and Likeness.

The Situation of the Russeting was such, that he was surrounded by Winter Pippins, Pearmains, and such-like; and we put the Master-Fruit together with several of the Changelings, as they grew on the same Branches mixed together.

This Instance will shew that Alteration may be expected in cognate Species; and I should have given an Example of a kind of Antipathy betwixt the Pear and the Apple in like Circumstances, but was disappointed. I am

Dear Cousin,
Yours, most obliged and affectionate,
B. Cooke

(Read Dec. 22, 1748.)

Vol. 46, p. 205-207:

Part of a letter from Mr. Benj. Cooke, *F.R.S., to* Mr. Peter Collinson, *F.R.S., concerning the Effects of the Mixture of the* Farina *of* Apple-Trees *and of the* Mayze or Indian Corn; etc.

When the Farina of one Apple impregnates another's blossom of differing Species, we see the Change in the Fruit; but whether any lasting Impression is left on the Bough which bore it (as seems to be in Tulips and some other Flowers), is not so easy to determine. Experiments of this sort being not to be made at all, but catch'd at

Mag. 2:454-476, 1748). Abraham Gotthelf Kästner entered the fray, upholding the theory of plant sexuality (*Hamb. Mag.* 3:11-24, 1749) Möller replied (*Hamb. Mag.* 3:410-455, 1749). Kästner returned to do battle (*Hamb. Mag.* 6:529-556, 1750). Möller again replied (*Hamb. Mag.* 7:428-440, 1751). This was one of the earliest of the many disputes over the sex of plants.

distant Opportunities; and till this Point is settled, the Distemper of my good Friend's Tree must rest unexplained.

Artificial Helps of sight have added to former Discoveries the Explosive Manner of the Farina's Action; but what may be the Effect of the inconceivably fine subtile Matter emitted from its Globules, and continually wafted about in great Plenty and Variety in the Summer Air, not only on the vegetable Productions (where on different Subjects it may not improbably have opposite Effects) but other Matters not yet suspected to be so much under its Influence, remains a Field of Inquiry for future Ages.—However, to what Mr. Loggan hath very justly observed (Transact. 440) on the Manner of Impregnation of the Seeds in Mayze—I can add this, that if the seed and whole Species of Mayze be planted about two Yards Distance from each other, there will be a Mixture of red and white Grains in the Ears of each Plant, and you may with Pleasure observe the Filament in the white Plant, which hath been struck with the red Farina, discovering its alien Commerce by a conscious Blush, and by counting the Threads they stained, foretell how many corresponding Seeds will appear red, at the opening of the Ear, when ripe.
(Read Nov. 2, 1749.)

Another reference to Cooke's hybridization is found in a letter of Peter Collinson to Sir Hans Sloane. The following extract is from p. 84 of *The Life of Peter Collinson* by Norman G. Brett-James.

I enclose an ear of corn from my cousin, Mr. Benjamin Cook, Newport, in the Isle of Wight. Pray be careful of the tenderfoot stalks of the wild oats, for the least accident may break them off the ear and then the curiosity is lost. Grain-bearing vegetables are furnished with seed vessels alike, and at the time of flowering, when the impregnation is made, the male farina of the wild oat, which grows in common with the wheat, did impregnate the pistillum of some of the forming grain in the wheat ear, which was very probably the way by which two different grains on the same ear received this information.[11]

[11] This explanation of Cooke is very different from that of Gerard, who reported the same phenomenon in 1633.

Johannes Gustavus Wahlbom

Wahlbom (1724-1808) published *Sponsalia Plantarum* (Wedding of Plants) in Stockholm in 1746. This essay was later included in the *Amoen. Acad.* Vol. I. The main object of the work was to describe the processes involved in the sexual reproduction of flowering plants. Wahlbom showed that the seed was analogous to the animal egg, both having to be fertilized before they could develop. He was interested in plant hybridization, but only as a final proof of the existence of sex in the vegetable kingdom. He reported a futile attempt to hybridize the banana, which failed because the pollen was abortive. He also wrote a short description of animal hybrids, which needless to say displayed a certain amount of credulity. He recorded very accurately the results of variety crosses in tulips, and he interpreted correctly the so-called degeneration in cabbage, which had been noted previously by Morison and Ray (page 77). The following quotations represent the major part of his contribution.

And so we are ignorant just how the generation is accomplished. When the horse cohabits with an ass, a hybrid species is produced, like neither father nor mother; however, there would be such a resemblance if either sex alone was the vehicle of the rudiment of the future fœtus.

If the *Canis aquatica graja* is impregnated by the *Canis aquaticus aviarius*, very often the female whelps are like the mothers, while the males resemble the sire. Faithful experience has shown us for a long time that the same thing happens when the *Gallina Frislandica* is impregnated by the *Gallus Gallinaceus vulgaris*.

An Æthiopian artisan, detained in the Hafnian prison, was fired with love for a slave girl and secretly raped her. Thence she became pregnant, and in due time brought forth a male child which resembled its mother inasmuch as the skin of its entire body was white, but the penis alone was black and showed the father's lineage. Barthol. Cent. 4, obs. 5.

All these instances show that the rudiment of the fœtus does not reside in the one sex alone.

The tulip hybridization is very clearly described, particularly the segregation of different types:

Tulip. Experimentation in horticulture is a pleasant thing: If perhaps a man delight only in a red tulip, let him pull off all the anthers on one flower before the pollen is scattered, then let him take a tulip with a white flower and sprinkle the anthers of this over the stigma of the red one, then when the seeds are matured, let him plant them in their own garden, and he will produce flowers in this garden, some red, some white, and many others bicolored, just as the offspring of two animals of different colors is born adorned in various hues.

In the next paragraph Wahlbom quotes from Morison by way of Ray. (See page 78.)

Richard Baal, a gardener at Bramford, collected in his own garden a large number of seeds from the *Brassica florida,* which he sold to gardeners, very many of whom lived in those suburban districts of London vulgarly known as "Neat Houses," and these men committed these seeds with the greatest of care and industry to earth well fertilized many years, but these seeds produced for them the large *Brassica longifolia aperta!* For this reason the aforesaid gardeners noting that they had lost their work and their toil, that is, that they had expended their industry, care, labor, and great expense without return, nay—with the greatest detriment and expenditure of time and money, started a lawsuit against the aforesaid Baal in the Court at Westminster, and the decision of the Judges sitting there not only condemned him to restore to them the money which he had received from them, but in addition that same Baal was fined that he might recompense the aforesaid gardeners for the waste of their time, their expense, and the use of their ground.

The above described misdemeanor must not be ascribed to the gardener, Baal, but to the fact that his *Brassicae optimae* were impregnated by the *Brassica vulgaris.* Wherefore, if anyone possess a *Brassica optima,* he must not let it flower in the same garden with

another, lest the better one be fertilized by the pollen of the poorer one, and from these seeds a poorer stock be produced.

These are two instances of hybridization so contemptuously and inaccurately cited by Sachs (Page 79).

Pehr Kalm

Pehr Kalm (1715-1779) was a celebrated Swedish naturalist and a pupil of Linnæus. He is remembered today primarily because he wrote an account of his travels in the New World, *En Resa til Norra America*, Stockholm, 1753-1761, a book which has been translated into many languages. Kalm set out on his journey in 1747, going first to England, and then in 1748 to the English Colonies in North America. It is interesting to note that he brought with him a letter of introduction to Benjamin Franklin signed by Peter Collinson.

During the next three years Kalm traveled extensively in Canada, New York, Pennsylvania, and the adjoining provinces, searching for new plants and collecting seed for European botanic gardens. He returned to his Professorship at Abo in 1751.

Kalm's brief description of hybridization in *Zea Mays* is to be found in a paper, *Beskrifing om Mays*, which he submitted to the *Kongl. Svenska. Vetensk. Acad. Handlingar* on December 14, 1750. This paper was published in two parts: part I in Vol. XII, p. 305-318, 1751; part II in Vol. XIII, p. 24-43, 1752. This contribution has recently been edited and translated by Miss Esther Larsen (*Pehr Kalm's Description of Maize, etc.*)

From Vol. 12, p. 308:

> . . . One does not see a sign of either male or female flowers on the former [the large variety of *Zea Mays*] when the small variety is in bloom. The large variety diminishes in height toward the northern limits of its range and finally it appears to lose itself in the smaller variety.

Differences in the color of the grains develop later. Although the majority of the ears have yellow kernels, some may have kernels which are white, transparent blue, brown, red, mottled, or red-and-white striped. The further south one goes, the more varieties of mays one finds, and more beautiful, showy, and numerous are the colors of the grains. The condition is quite the reverse in the north, for in Canada one hardly sees any but white, light, or occasionally blue mays. The small variety does not produce as many colors as the large. At times some of the grains on an ear of corn are yellow, while others are red. This mixture is brought about by the planting, for it is to be noted that if yellow and red varieties of mays are planted close beside each other, the ears which grow on them will have a mixture of red and yellow grains. This mixture is due to the fact that at the time of blooming, the winds blow the pollen from one variety to the other. One might also get a mixture if one planted the three-month variety beside the tall form, although the three-month mays usually blooms before the other. He who wishes to keep mays unchanged must be careful not to plant different types next to each other.

William Douglass

William Douglass, M.D. (c. 1691-1752) was born in Scotland and probably obtained his medical degree from the University of Edinburgh. He migrated to the New England Colonies and spent the remainder of his life as an active physician in and about Boston. He soon became a real leader in his profession and was the first to write an accurate clinical description of scarlet fever. At odd moments, when he could find the time, he wrote *A Summary Historical and Political of the First Planting, Progressive Improvements and Present State of the British Settlements in North America,* which was published in Boston, the first volume in 1749, and the second in 1751. Two later editions were issued in London in 1755 and in 1760. A short footnote in Volume II contains Douglass' contribution to plant hybridization.

In describing the products of Connecticut (Vol. II, pp. 204-205, ed. of 1760) Douglass wrote,

. . . it [maize] emits its coma, plume or blossoms, end of June; then they cut off the top of the stalks, that the grain may receive the more nourishment.[e]

The footnote follows:

[e] Here the farina fecundans of vegetables seems to be evinced: this plume or flower, if cut off before its maturity, the maize bears no ear or grain. In New England where the grain is of various colors (white, yellow, reds of several shades, blues of several shades, marbled, and mixtures of these in the same ear) the grains planted of various colours, and in the neighborhood receive alterations in their colours and shades by the various impregnations; this is observable also in other vegetables, beets, carrots, & C.

This passage, together with the contributions of Mather (1716), Dudley (1724), Cooke (1749), and Kalm (1750), indicates that the spontaneous crossing of color varieties of *Zea Mays* was well known, at least in the American Colonies. The limitations of plant hybridization, however, were little understood. Pollen seemed to be merely a general fertilizing substance, and consequently even plants in different orders were thought to cross spontaneously. When we consider the state of botanical knowledge in 1750, we must treat such speculations as the following with a certain amount of respect. From p. 206:

New England wheat is subject to blast; some think that it proceeds from the *farina fecundans* of the barberry bushes.[12]

Just how the barberry pollen blasted the wheat is not stated. It was generally believed that pollen affected the tis-

[12] It was not until 1865 that De Barry proved that barberry and wheat were the alternate hosts of *Puccinia graminis*, the fungus which causes the black rust of wheat. For many years, however, the farmers had suspected that there was some connection between the barberry hedges and their diseased crops. At Rouen, France, the growing of barberry was forbidden in 1660, and in Denmark the peasants noted that wheat rust was more severe in the vicinity of barberry about 1805. Early in the eighteenth century several of the New England Colonies had forbidden the planting of barberry, and Douglass quotes a Connecticut law which commanded its destruction because it was thought "to be very hurtful by occasioning, or at least increasing the blasting of the English grain."

sues of the maternal parent; and thus barberry pollen supposedly could poison wheat by an extension of what we would call metaxenia. On the other hand it is possible that the farmers thought that their wheat merely suffered from a sort of vegetable hay fever.

Johannes Haartman

Haartman (1725-1787) published *Plantae Hybridae* under date of November 23, 1751. It was printed in the *Amoen. Acad.*, Vol. III. This work describes a number of different hybrid plants, and it is one of the few contributions to the subject which has not been overlooked. Haartman himself did not attempt to cross different varieties or species, but seems to have been content with identifying certain plants as hybrids on taxonomic grounds. Undoubtedly some of the plants he described were actually hybrids—*Veronica spuria*, for example—but many of the so-called hybrids certainly could not be descended from the parents to which he assigned them. The pollen of *Rhus toxicodendron* could hardly have fertilized the flower of *Actaea spicata*. Certain hybrids, however, are very carefully described, and the plate illustrating the offspring of *Veronica maritima* × *V. officinalis* is perhaps the first accurate picture of a known hybrid plant.

Haartman, after a brief description of the sexual nature of the flowering plants, proceeded to a discussion of hybridization:

> Moreover, it is very well known to anyone at all curious that animals very rarely have sexual intercourse outside their own kind, but nevertheless it is much rarer for them to procreate that bastard offspring which is called a Hybrid. The mule, generated as it is from two different species, the ass and the mare, proves that hybrids are a possibility. We have an equally clear example of a hybrid in the realm of birds, when, in the case of *Passer Canariensis* cohabiting with the *Carduelis Fœmina*, from that union are sprung sons and grandsons (but no great-grandchildren) and they turn out like their father and

their mother. Nor can we in this regard pass beyond those stupendous limits prescribed by God, for the birds that result from that union are a hybrid species even if they are furnished with organs of generation, for they can scarcely, and eventually not even scarcely, propagate their families.

Whether hybrids of this sort are also in existence in the vegetable kingdom has, up to this time, not been sufficiently apparent in examples, since the laws covering the generation of vegetables were first clearly recognized in this century. Besides, Vegetables are so changed by the climate and the fertility of the soil that one and the same plant, born in different earth, very often seems to be a variety entirely unlike its parents.

But if I am asked whether new species of plants can spring into being through mixing two distinct varieties, or whether they do appear daily, I would reply to these questions that in accordance with theoretic principles, and as far as we can discern with our eyes, I would freely declare my opinion by denying it. For not only do we see the rudiment of the seed in the germ cell long before the time of fecundation, for we even see the outer bark turn into the calyx, the inner bark into the Corolla, the wood into the stamens, and the marrow (medulla) immediately transformed into the very seed. Even in grasses and other Monocotyledons I find that the medulla is continued from the root into the seed itself, and the pulpy material there is loosened when the seed falls down. When the seed sprouts from the earth, it too grows and sends out rootlets in that spot where it had been torn off, so much so indeed, that I willingly consider it as certain and indubitable that the embryo lies hidden before fecundation in its germlike medulla. I see, indeed, that no seed germinates before fecundation, that the pollen clings to the dewy stigma under the flowering parts, is broken there, and the content of the pollen is absorbed by the pistil and comes thus to its seed. Nevertheless, I would readily agree with Nedhamius in making this first movement of the seed nothing else except an elastic something, *if the hybrid species of animals, which aspire to the likeness not only of their mother, but of their father as well, did not persuade one differently.*

The chief argument for believing in hybrid plants, however, seems to be corroborated by the following. For all agree that Botanists such as Tournefortius, Boerhavius, Mitchelius, Pontedera, and Helwingius,

with the rest who lived at the end of the last century, and indeed in the time of our President in this century, have collected innumerable new European plants, unknown to the ancients, but it must be observed that these plants are for the most part so like the old ones that they can scarcely be distinguished by form. And so when differentiating characteristics were sufficiently absent, our President referred to their mother plant under the name of varieties, which differ in color, odor, taste, size, time of maturity, etc., and the most acute of the Botanists, like Jussieu, Ray, Gronovius, Haller, Gmelin, Guattard, Dalibard, Wachendorff, Gorter, Bütner, etc., also approved this practice and continued it after him. Indeed it has been said that these varieties arise from the condition of their soil, place, or climate, and to that extent only are accidental. Meanwhile, however, to this reformation were subjected many plants, which had often been a source of the greatest anxiety to botanists in the determination of their species, and to which species they deserved to be referred, when they resemble two different species, especially when the distinguishing characteristics of the plant in question are found not to be unique, yet very distinct and very individual or absent in either of these two species they resemble. And this hybrid grows in the same soil with both the species and yet was not observed by the ancients. And this circumstance first led us by deduction to this problem, whether two different plants have produced a third and whether the third plant is to be considered a hybrid, for botanists have first recognized with clarity in these times of ours the principles governing generation in plants, and such changes in plants may be deduced from what they have observed in the *Brassica* and others.

Since nature is very opulent and various in her operations, I would almost believe nothing except that which can be shown by experimentation or can be touched with the hands, and therefore I now advance to the effects of nature, ready to examine whatever she has proved. But meanwhile let the reader not allow himself to be completely frightened away by this unexpected doctrine as though it were new and absurd, since we have noticed that other men too have but recently suspected that this, as it would appear, preternatural happening is simply a result of the mixture of two species, and to prove this Marchand alleged the unique example of the *Mercurialis* with the lappet leaves which he thinks derives from a father unlike itself, but

which nevertheless propagates its species. Our noble lord President, in his dissertation on *Peloria*,[13] has adduced certain examples which seem to show that hybrids are produced in plants as well as in animals. The celebrated master Gmelin seems to have observed the same thing in the case of certain *Delphinia*.

A part of Haartman's summary follows:

In order that our demonstration, supported by examples, since in natural sciences principles of truth ought to be confirmed by observations, should end more clearly, let us divide plants into certain groups.

I. Bigeneric plants born from different genera:

1. Veronica	2. Arctotis	3. Delphinium
4. Poterium	5. Ascelpias	6. Saponaria
7. Primula	8. Aquilegia	9. Chelidonium
10. Tragopon	11. Blitum	12. Dracocephal
13. Cochlearia	14. Brassica	15. Arundo
16. Syringa	17. Actaea	

II. Congeneric plants born from different species of the same genus:

18. Verbena	19. Helianthus	20. Trifolium
21. Centaurea	22. Rhus	23. Carduus
24. Tussilago	25. Dipsacus	26. Urtica
27. Pyrola	28. Thalictrum	29. Thalictrum
30. Antirrhin	31. Alchemilla	32. Iris
33. Veronica	34. Carduus	

III. Plants described by odor and irregular shaping:

35. Mentha	36. Tenacetum	37. Malva
38. Malva	39. Reseda	40. Geranium

IV. Obscure plants, where ancestry is ascribed with difficulty:

41. Acanthus	42. Acanthus	43. Cynara
44. Moluccela	45. Dryas	46. Rhinanthus
47. Menycanthes		

New additions to the problem just investigated:

1. It is certain that there is such a thing as hybrid generation in animals:

[13] The article on *Peloria* is signed by Rudberg. The fact that Haartman credits Linnæus with the work shows that possibly the teacher rather than the student is responsible for the contribution.

Example—Mules are born from the mare and the ass, but there is not a second generation.

The union of the *Passer Canariensis* and the *Carduelis* produces a first and second, but no third generation.

2. It is equally certain that there is such a thing as hybrid generation in plants:

Example—The *Mercurialis annua* with cloven leaves (*Act. Paris* 1719) which perishes.

The *Veronica spuria* with abortive flowers which does not die out.

3. Homogenous plants are very easily mixed at the time of fecundity:

Example—*Brassica* with *Rapa* and *Napum*—certain.

4. Unrelated plants are mixed more rarely, but occasionally:

Example—*Veronica spuria* (I) undoubted.

5. When unrelated plants are mixed, the *Mercurialis* and *Veronica* (2) show that the structure of the fruit-bearing organ in the daughter is like that of another plant. It is a matter of note that accidental attributes, such as color, size, odor, taste, fullness, are not included by Botanists under "structure."

6. When either unrelated or homogenous plants are intermixed, the *Veronica* is an evidence that often the Herb of the daughter is like that of the father.

7. This is illustrated by examples. When the rabbit forces a hen, the hatched pullet is a woolly cock, as Reaumurius[14] has observed. The plant is the state of maturity, the Herb is the larva of the plant, as in the case of insects.

The life of the plant is the Medulla, which is continued down into the seed, which is first fertilized by the staminal part of the cortical substance.

[14] Renati Antonii de Reaumur (1683-1757) was one of the most versatile scientists of his time. He invented a thermometer and an incubator, and he wrote an excellent natural history of insects. The incident referred to by Haartman is described by Reaumur in *Art de faire éclore les oiseaux domestiques*, Paris, 1749 (Vol. II, p. 354), and in the English edition, *The art of hatching and bringing up domestick fowls*, London, 1750, (pp. 450-456). The rabbit and pullet were kept under observation almost continuously for three months and the coition was actually observed. The eggs laid by the pullet, however, failed to hatch.

8. Further lively experimentation is desired on more hybrid plants which are fertile and bear seeds.

9. It is not true that the varieties of plants arise from conditions of soil and hence can be changed by cultivation.

The Pæonia or the double Narcissus is not changed by virtue of its soil into the single nor for that reason are they diverse in species.

10. It is not strange that a hybrid which is the child of a swamp and a mountain plant should seek a third kind of soil. For this reason the grandfathers and great-grandfathers are sought in vain next to the daughter plant.

All these things we have proposed hypothetically, for we see them from afar, very remote, as it were, and very small, although in themselves they are very great, but the centuries will reserve them for the botanists not yet born, who, when they have reached that point, may rear on this foundation a reformation in the whole science of Botany, and may distinguish the varieties of the species far differently from us, and perchance they will determine the genera of plants differently, too.

Haartman was the authority for the brief statement concerning plant hybridization made by Petro Bremer in his dissertation *Somnus Planatarum*, Upsaline, 1755, and reprinted in *Amœn. Acad.* IV. A review of Bremer's article in The Gentleman's Magazine (27:315-320) of 1757, contained an almost literal translation of his remarks on plant hybridity. From page 316:

That the flowers of some species are impregnated by the farina of different genera, and species, inasmuch that hybridous or mongrel plants are frequently produced, which, if not admitted as new species, are at least permanent varieties.

Christlob Mylius

The versatile Christlob Mylius (1722-1754), author, journalist, and editor, founded *Physikalichen Belustigungen* in 1751. In one of the early numbers (Vol. I, pp. 81-96) of this periodical, appeared an article entitled *Von Datteln, welche auf eine merkwürdige Art reif, geworden.* Although this

paper was unsigned, there is little doubt that it was written by Mylius himself, for it was assigned to him by his contemporaries, von Gleichen and others. The greater part of the contribution is taken up with a description of Gleditch's successful attempt to fertilize a female date palm in Berlin with pollen brought from a male tree in Leipsic. The last two paragraphs, however, describe hybridization within the genus *Brassica* and discuss the question of crossing different species of plants. The pertinent excerpt follows:

It often happens, that when one sows the seed of white or brown cabbage, a type of cabbage comes up which is neither white nor brown. Kitchen gardeners call it *Schalkkohl*. Does not this arise through either the impregnation of the female flowers of the white cabbage with the masculine flower dust of the brown cabbage or the impregnation of female flowers of the brown cabbage with the flower dust of the white cabbage? This conjecture appears to be strengthened by the similar experience of Herr Michelmann. He had planted Savoy cabbage (yellow Welch or *Wersichkohl*) and brown cabbage side by side. When he had sown the seed which these produced he obtained a kind of cabbage which could be described as reddish Savoy cabbage. For it had the reddish color of the brown cabbage and the curled leaves of the Savoy. Who would not be led to believe from this experiment that this new cabbage arose through the impregnation of one cabbage flower by the masculine flower dust of the other?

If one supposes that the seeds of plants are fructified by the flower dust, he can understand whence come the almost limitless variations. It is not improbable that from this straying of the flower dust have arisen not only many varieties but also many species of plants, which previously had not existed. But it is hardly believable that new genera should arise in this manner. Indeed one sees many plants degenerate so that it cannot be determined if they belong to a certain definite genus. Herr Linnæus recorded in his *Amoenitatibus academicis* (pp. 55 ff.) many beings from a plant newly discovered in Sweden. He himself saw that they must have arisen, considering all the circumstances, through the mixing of a certain plant with *Linaria*. Likewise he made a special genus for them and called them *Peloria*. From

Upsala however he recently announced that this plant was only a variety and had already degenerated again.

Edme Gilles Guyot

In 1752, Monsieur Guyot (1707-1786), an amateur botanist and an employee in the French Postal Bureau, published an article on the color of flowers. This contribution, entitled *Sur les fleurs et sur les causes de la variete de leur couleurs* was printed in the *Observations sur l'histoire naturelle, la physique et la peinture* (Vol. I pt. 1, p. 75). This short memoir contains directions for cross pollinating flowers of different color varieties. Apparently M. Guyot had crossed a number of horticultural strains and had obtained hybrids, some of which were variegated, while others were of a color intermediate between the parental types. The conclusions drawn by M. Guyot cannot be accepted *in toto* however, for he was ignorant of dominance and of Mendelian segregation. Then, too, we know nothing of his records or how carefully each particular cross was made. Nevertheless there is no doubt that he was a practical plant hybridizer.

M. Guyot's contribution seems to have been alternately forgotten and remembered. Gärtner referred to it briefly in 1848 and Edouard Morren quoted it extensively in his *Dissertation sur les feuilles vertes et colorées*, Gand, 1853. In 1858 the entire article was reprinted in *La Belgique Horticale, 8:106-112*, and recently Lehmann (1916) called attention to it and quoted certain passages which described hybrid flowers. As this paper is an excellent illustration of the widespread knowledge of plant hybridization in the middle of the eighteenth century, it is reprinted here in full.

On Flowers and the Cause of Variety of Their Colors

By M. Guyot.

The extreme care which has lately been taken in cultivating flowers, and the natural mixing of different colors which occurs when

they are seeded, have enabled us to raise flowers which surpass by far those which have been cultivated in the past. *Tulips, Primroses, Ranunculi,* and *Anemones* were certainly not as beautiful sixty years ago as they are now. The most beautiful of all of the older ones would be utterly rejected today. It is commonly believed that it is only by seeding and selecting flowers in the same species, without regard for their color, that we have succeeded in raising those that have acquired the most brilliant varieties in the tints which characterize them. I say, on the contrary, that up to the present the combinations which have been made by chance have done more to produce the different kinds of color which are found in flowers, and that culture has served only to give them a more beautiful form. It has not been realized that there is nothing easier than to raise flowers of the desired colors, and I am now going to demonstrate how it can be done.

I intend to speak here only of the species of flowers cultivated by amateur florists. These flowers are Tulips, Anemones, Primroses, Hyacinths and (*Semi-doubles*). I made my observations on these species and I shall attempt to explain their infinite varieties.

M. Geofroid[15] the younger has given us a new conjecture on the generation of plants; he claims that the dust from the tops of the stamens of the flowers, falling on their pistil, procures the fertility of their seeds, and if one cut off the stamens from the flower as soon as they appear, the flowers will not give any seed.

From thence I am led to believe that the stamens planted near one another procure their fertility reciprocally, and that if the parental flowers are of different colors, the colors of those which will come from their seeds will be a mixture of those that have procured the fertility of the seeds. This cannot take place between plants of different species; but bizarre flowers will arise from the mixing of varieties, and they will take their nature and color from the plants whose staminal dust has contributed to the fertility of the seeds.

It follows from this opinion that two flowers of the same species, but of two different colors, planted beside each other and blossoming at the same time, must produce a plant of the same species, whose flower-color will contain a blending of the colors of those from whose stamens the dust has contributed reciprocally to the fertility of the seed.

[15] Monsieur C. J. Geoffroy le jeune.

To be assured of the truth of this conjecture, which, as I will make plain afterwards, seems reasonable enough, it is only a question of making flowers bloom when mixed together in an out-of-the-way place. The flowers must be of the same species of pure colors, simple and seed-bearing, for example, half of them red and half yellow. The seed which comes from them must be planted separately and it will then produce flowers colored red, yellow, and orange, since orange is produced by the mixing of red and yellow. Some flowers will even be found in the medley, produced by these two first-colors, which will be checkered with orange and red.

To perform this experiment with more precision, it is necessary to make the flowers bloom as much as possible together and on the same days; this is done very easily by cutting back the flowers from that plant which would produce more than the other; by this means the time of the flowers' opening will be delayed to make these flowers bloom the closest that is possible.

If the opinion of M. Goefroid is true, ranunculi coming from seeds one has gathered will be of the colors indicated above or colors closely approaching them. If on the contrary the said seeds produce plants of a violet, purple or white color, there will be some place for doubt in this communication.

For a counter-experiment, one can make the flowers of the above colors blossom separately and far away from each other, and plant their seeds separately; each will give flowers of its own color.

These experiments are easy to do and will suffice for an assurance of the truth of my opinion.

There are some general observations that I have made on flowers which confirm the particular experiment of which I have just spoken. I have planted seeds of the different species of flowers detailed above and I have succeeded in raising flowers of colors mixed and combined. For example, I sowed a thousand seeds of Auriculas of different colors; those which have come from them have borne flowers of colors which were mixtures and blends of the colors of those I had planted, yet among them there never have been found two which were exactly alike, they were all more or less blends of the colors of the flowers which had borne the seeds. With the little that is known of mixing colors it will be easy to conceive this combination.

I observed that when I sowed the seeds of the red, purple, violet, and white Auriculas, those which came from their seeds were never blue or green, which conforms to the nature of the colors, seeing that blue which is a primitive color cannot be produced by the mixing of some of its colors, and that green can be produced only from blue and yellow: But the flowers which came from this mixture were either crimson, being produced by the intercourse of the stamens of violet and flame-colored flowers, or straw-colored, produced by those of white and yellow flowers, etc.

The Author of nature, whose wisdom has foreseen all, has created very few species of flowers of a blue color: and it is easy to note that the same species of flowers which are blue in color are never at the same time yellow, which would have produced, by the mixing of the colors, flowers quite green, which would not have been at all agreeable to the sight and which then might have been confused with the leaves of the very plant which produced them.

Those who cultivate flowers and think that they can raise blue ranunculi are wrong, because there is no color in the ranunculi which in mixture produces blue; if there were any of this color in the beds and if they had communication with yellow ones, they would produce green flowers, very disagreeable; and moreover blue flowers would produce dull and dirty colors in combination with most other colors, and then we should no longer get flowers of pure red, yellow, and orange. These species would be corrupted and spoiled by a single mixing with a blue color which is not analogous with red or orange or yellow.

Hyacinths are all either blue or white; some have a little rose color; there is no danger that the mixing of these three colors can produce anything disagreeable to the sight, from them will come only Hyacinths which are more or less pale or deep blue, or violet-blue or variegated blue and white. Yellow Hyacinths will never be produced, these three colors can not produce yellow in combination. And this is also true of larkspur, which has the same three colors as the Hyacinth.

Anemones are in general violet-blue or crimson-red; they are not pure red[16] or orange or yellow; and in one word, when a species of

[16] By pure red is meant the color of scarlet or vermilion.

flower produces yellow colors it does not produce blue ones; when it produces blue ones it does not produce yellow ones; but it must be observed that in all species violet-purples and crimsons are found, because these are not primitive color and their mixture with blue on the one hand and yellow, orange, and red on the other can produce neither a perfect green nor disagreeable colors. Primroses of an olive color are found, but they are produced by the mixture of violets and yellow.

If one believes that flowers do not communicate their color to each other at all, in spite of what I have explained above, let him tell me then why in the same species of flowers which are blue in color, there are never any yellow ones and why among the yellow ones are never any blue.

It follows naturally from what I have just said and from what I have experienced, that flowers of a different nature, like the ranunculus and the anemone, etc., never communicate their colors to each other. If it was true that the dust from the stamens of a yellow Narcissus could contribute to the generation of the seeds of a blue Hyacinth, there would be produced green flowers which would take their nature from the Hyacinth and the Narcissus: this has not yet been seen and so-called chance has not yet produced it.

It can be concluded from all that I have just said, that it is not difficult to raise flowers of a desired color, or very near it; it is enough to have a certain number of simple plants which bear seeds and are of primitive colors, namely red, orange, yellow, white, and violet on one hand, and blue, violet, crimson, white, and brown on the other, to give colors which are more or less light or dark.

If one wishes to raise sulphur-colored ranunculi, he will plant white and yellow ranunculi in one box and sow the seed that they produce, which ought to give ranunculi that are sulphur-colored or streaked with white.

If one wishes to have gold-colored ranunculi he will plant red and yellow ranunculi of a gold-color or variegated yellow and red; and the same way for others.

It is necessary to take pains in making these experiments, and one cannot dispense with keeping exact notes of the procedure followed.

I will not demonstrate here the manner in which the dust from

the stamens of one flower, flying through the air, operates upon the pistil of a neighboring flower; that belongs entirely to Physics, and besides, that which I could say would be only very abstruse and uncertain. It is enough for me to point out that they act effectively and communicate the color of their flowers; it is only by repeated experiments that one can assure himself more and more of the truth of this opinion.

In each of two species of flowers two sorts are distinguished, the pure and the streaked; the pure are of only a single color and the streaked are of two or three colors.

This difference between flowers which are pure and those which are streaked comes, I believe, only from the fact that, in the pure ones the colors, either clear or obscure, are completely mixed and blended with the fundamental color of the flower. These colors are always either white, red, orange, and yellow on one hand, or red, crimson, and violet on the other hand. In the streaked flowers the colors are separated and distinguished from each other, for the colors which form the streaks are not fused with the fundamental colors.

In the Tulips which are called *colored*, the colors which are to form the streaks are more or less deep red, such as the purple or the violet. These are blended and mixed with the fundamental color of the Tulip, which is always yellow or white; it is only after many years of repeated planting that the colors forming the streaks begin to separate from the fundamental color and thereby form those admirable varieties which are the merit to the Tulip.

The fundamental color of the Tulip which is always either white or a more or less golden yellow is thus extended all over the petals and the colors of the streaks is blended with it only in planes; this is why no Tulip ever has streaks of its primitive color. When the base color is yellow, it varies in depth as yellow blends with the red and the violet; the paler the yellow, the more the colors of the streaks approach red or violet; the more golden the yellow the further removed are they from these colors.

When the basic color of the Tulip is white, the color of the streaks is red or violet, more or less light or dark, or purple and crimson which is produced by the mixing of these colors and white.

Many authors have imagined that Tulips become streaked with

old age; I am not wholly of this opinion. A Tulip becomes streaked, I believe, as it detaches and separates the little particles which form both the color of the streak and the basic color of the Tulip, from the juices that it receives with more or less abundance. When the flower becomes streaked the particles of the nourishing juices run freely along the fibers which go out from the foot of the vase of the Tulip and extend the length of the flower petals: these colored particles (let us suppose violet) were blended and mixed with the basic white of the flower, before the Tulip became streaked, forming a Tulip of a pale Violet color; but if then they happen to approach one another, they give in these places a brighter and deeper color and form the agreeable variety that we see in Tulips. Places where the violet color of the streak is of a black violet are those where these particles have accumulated most, and are as if congested in the fibers of the petals.

Often a streaked Tulip becomes pure, doubtless because the color of the streak becomes blended again with the basic color of the flower; the quality of the earth or the too great abundance of sap can produce this effect.

Application to Violets

Violets become streaked ordinarily from the first year, and when once the streak mingles with the basic color it does not separate.

There is every reason to believe that when the particles which compose the streak of the Violet are blended in the sap with those of the basic color, then the layers that they produce can no longer separate the colors to form the streak.

This in general is most probably all that can be said about the formation of streaks in flowers. I leave to the amateurs, who wish to make the experiments of which I have spoken here, the liberty of doubting all that I have just reported until they become convinced on their own account, and I beg them to be kind enough to suspend their judgment until then. Nevertheless I shall always be very flattered if the most intelligent wish to do me the honor of communicating their opinions to me.

For many years Violets have been raised whose basic color is yellow; they are not a beautiful yellow; but if their culture is continued there is every reason to hope that there will result Violets whose basic color

is of a different yellow, in the same colors as the Tulips whose background is yellow, since Violets with a white background have the same streaks as the Tulips of this color.

James Parsons

James Parsons (1705-1770) was a philosopher of a type which was abundant in the eighteenth century but is now almost extinct. He illustrates the danger of mixing theology with the natural sciences better, perhaps, than any other man of his time. His remarks on plant hybridization are neither extensive nor accurate, and they have no intrinsic value; nevertheless they give us an interesting sidelight on the attitude of some of the early naturalists.

Parsons published the *Philosophical Observations on the Analogy between the Propagation of Animals and that of Vegetables* in 1752. In his discussion of hybrids he mentioned briefly the sterility of mongrel plants, and it is evident that he believed the inability of heterogenous organisms to reproduce themselves to have been arranged by the Deity to prevent monsters from perpetuating their kind. He stated the dogma of the constancy of species very clearly, and he assigned human beings one unique advantage over all other forms of life. From page 97-101:

. . . Now by this admixtion and combination of these refined Fluids, which we have often call'd an *Effluvium* in the Male Parts, there is an immediate alteration produced that was not existant in the *Ovum* or *Seed* before; for the innate Juices of the Organization has Qualities peculiar to itself, as to *Colour, Taste, Smell,* etc., be its Quantity never so small; so no one can in the least doubt, but the impregnating *Effluvium* of the *Male parts* of Animals and Vegetables has its own peculiar Qualities, as to *Colour, Taste, Smell,* etc. . . . Now, therefore, it can be no difficult matter to conceive how the Congress of *Black Man* with a *White Woman,* or *vice versa,* should propagate a *Proles* of a Colour between both; the common Experiment of mixing what we call a Flesh-Colour and Black, in certain Proportions, will

produce a *Tawny*, and in a great measure also influence its Form, as it grows. And thus in Vegetables, if the *Farina* of one Species of Plant or Tree should reach the Flower of another, and fœcundate the *Ovarium*, the colour of the future flower and Fruit would be variegated, and the Form of the Fruit a great deal influenced too.

It is impossible to omit making an Observation in this place of the Benignity of the *Divine Being*; in this very Matter he seems to have done every Thing that might favor the Propagation of the *Human Race*; for tho' such different *Species* of Man and Women sometimes meet, and copulate, there is such an agreement between the *refined* Parts of the seminal Matter of the Male and *innate Juices* of the Organization of the Female, that there is nothing in their commixtion which can prevent the *Proles* from being capable of further Propagation, with any other different *Species* of the Human Race. Whereas when different Species of Animals copulate, for Example, a Male Ass and a Mare, their Proles cannot produce another Proles of any Kind.* This *Phaenomenon* has not been hitherto accounted for, that I know of; but I shall attempt to account for it by offering Reasons, as follows: the Impregnating *Effluvia* in the seminal Matter of the *Mule* are so much degenerated, by the former unnatural Mixtures of the Parents, from any *Homogeneity* with the Particles of the innate Juices of the Organization in the Ovum of its Female, or any other whatsoever, that, instead of that Agreement that naturally happens in the Fœcundation upon the Coit of homogeneous Animals, the Access of those *Effluvia*, in such as are *heterogeneous*, either utterly destroy the Organization, or they have not the proper *Qualities* for promoting any further Propagation, and so leave the *Ova* unimpregnated, and consequently incapable of ever coming to any Thing.

From these Considerations it plainly appears, that the Design of

* Even tho' it is affirmed that the male and Female *Mules* are as salacious and eager for the Coit as the most natural Animals; in like Manner such Fruits or Seeds as may be product of a preternatural Coit, would also be incapable of producing a Succession of others like themselves; the Number of the Species of Plants was limited at the Creation, as well as that of Animals; and the same Disagreements of the impregnating *Effluvium* of the Globule of Farina would happen, by any accidental Excursions from their own natural Course with the Juices of a different Organization, and their successive Powers and Qualities would inevitably be destroyed.

Providence was to imprint such restrictive Laws upon those Parts of Nature, that are to be propagated in Succession to each other, as are sufficient to render them all Beautiful; to preserve their natural Forms; to prevent and hinder the Propagation of a Race of Monsters† upon the Earth, in thus altering the Nature of the *Effluvia* mention'd, by a preternatural Coit of Animals; and very effectually and particularly to favour the Propagation of the Human Race, let the People, which come to-gether, be never so different in their Persons; all which will gradually grow more evident in the Sequel of this little Work.

Johannes Gessner

Johannes Gessner (1709-1790) was Professor of Mathematics and Physics at the University of Zürich. He made a number of contributions to the science of botany, and became a close personal friend of Linnæus and Von Haller. Indeed his *Dissertations de partium vegetations et fructificationis structura, differentia et usu* was published twice by Linnæus; the first time in the *Oratione de peregrinationibus intra patriam,* Lugduni Batavorum, 1743 (pp. 55-108), the second time in the *Fundamentis botanicis,* Halae, 1747 (pp. 33-78).

Gessner's discussion of plant hybridization is in the *Dissertatio physica de Ranunculo bellidiflora et plantis degeneribus,* Tiguri, 1753. In this work Gessner attempted to explain the occurrence of two different species of flowers upon a single plant. The opening paragraph describes the occasion:

In the month of May in the year which has just elapsed [1752], my very honored friend, D. C. Gossweiler, an outstanding Botanist and contributor to the album of the *Societatis Botanicae Caesareae Florentinae,* sent me an unusual spectacle from the vegetable kingdom, a specimen, undisputably *Ranunculus minimum pratensem,*

† If it was not so, we should by Degrees see a new Set of Heterogeneous Animals and Vegetables arise upon the Earth; but it is plain it was never the Design of the Almighty, since every Species of Animals and Vegetables are the same now that they ever were, nor must we expect any others, while time subsists. See my *Mechanical and Critical Enquiry into the Nature of Hermaphrodites,* Chap. I. p. 7.

bearing among the *Ranunculus* flowers one like the flowers of the smaller white daisy.

The plant is next pictured, described, and identified, and the whole question of degeneration discussed. This leads naturally to a description of the sexual methods of propagation, by seeds, cuttings, etc., and to some speculations as to the causes of variations. The existence of mutations is admitted and the well-known case of *Peloria*[17] is reëxamined. Degeneration caused by transplantation is next compared with spontaneous mutations, and finally the rôle of hybridization in the production of new varieties is evaluated. Section XIII bears the title *Degenerationes ex copula plantarum & variae plantae Hybrida.* The opening passage of this section is translated as follows:

Some degeneration is caused by the cross fertilization of Plants. Fertilization is secured through the passage of the influence of the anther's pollen to the rudiments of the seed located in the bud. This fertilization gives to the seed, the stalk having opened, the ability to begin the life of the new plant. It is not easy to determine what the reason for this is. It can be said, however, that from this pollen alone comes either the energy of development or the beginnings of the organic part. These plant rudiments, however, are also formed in the buds and roots without the aid of masculine seed. But in the seeds, the embryos do not grow without a preceding fertilization, secured through the pollen from the anthers clinging to the pistil. This has been demonstrated today by many experiments. This fertilization produces variations through the coupling of different forms, either through the masculine powder going to a different species of the same genus, or finally, to a different genus. Hence it is necessary that new plants appear, which are very different from their original parents, and which assume the form of new species bearing, however, the common characters of the two [parent] plants, some in the vegetative parts, others in the fructification. Authors have recently taught this through many examples and arguments. . . .

[17] See Rudberg (p. 149) and Stehelin (p. 153).

Gessner then proceeds to quote Haartman (p. 167), Gmelin (p. 154), and Browall[18] and to cite the classical records of degeneration in plants. He ends the essay by summarizing the work of Haartman and Marchant (p. 122), and states that he intends to experiment with artificial hybrids.

Nicol. E. Dahlberg

Dahlberg, the fourth of Linnæus' students to discuss hybridization, published *Metamorphosis Plantarum*, Upsaliae, June 3, 1755. The essay contains a description of metamorphosis in insects, and a number of citations by authorities who had reported that frogs sometimes changed into fish. Morphogenesis in plants was discussed next, and these developmental changes were considered to be only another form of metamorphosis. Changes due to spontaneous hybridization were noted also, and the results of species crosses in both animals and plants were described in a section appropriately labeled "Alienations." Although Dahlberg had more than his just share of credulity, he does exhibit traces of a healthy skepticism, which is especially noticeable in his citation of the peculiar experiment of Reaumur. On the whole his dissertation contains an excellent sample of what educated people of his time believed concerning hybrids.

After the sex of plants, or rather their fecundation, had been established so clearly before their eyes that almost all the world could see it, and observations in this direction had been adroitly set into motion, the Botanists found that hybrids were occasionally produced in plants just as in animals, when the third plant comes forth from the union of two distinct plants, as the Mule is born from the Horse and the Ass. Animals which result from a mixed union rarely propagate their own kind; it is still uncertain whether this law is of equal validity in plants; it is sometimes affirmed and sometimes denied by those plants which botanists have observed up to now. If now it is so (which seems very

[18] Johann Browall, *Specimen de Transmutationes specierum in Regno Vegetabile*, Aboae, 1745. I have not been able to consult this paper.

probable) that many hybrid plants are propagated by seed, they may occasionally achieve the status of the constant varieties, and for this reason a new metamorphosis in plants is effected.

These constant varieties (to which *Sedum Telephium*, the *Serapias helleborine*, and many other plants belong) which are now disturbing Botanists very much, may possibly be explained occasionally in accordance with the principle of sex in plants and hybrid generation. The *Gallina Frislandica*, or "crispa" [curly], with bent-back feathers, and no plume, having been dissected, even to the smallest parts, by the anatomical knife, and examined by a certain very perspicacious anatomist, cannot be of one and the same species with the common hen, although its feathers are curved back and it transmits its characteristics to the offspring unchanged. When the celebrated Reaumur permitted a rabbit to cohabit with a hen,[19] the eggs turned into pullets very like the hen, but they did not have feathers, but were covered with soft down; this experiment in some fashion indeed points that way; [that is, to the variety of interbreeding], but from this one instance we do not dare to make conclusions as to the universals, for from it horrible conclusions may be drawn, and an occasion given to those who believe that the Moors among men have some such singular origin which, however, I am unwilling to attribute to them.

In our country a certain tree appears, though rarely, which is a sort of a cross between the *Pinus sylvestris* and the *Pinus abies*, that almost no one could determine what species of tree it might be; for it has long branches like ropes, and the whole plant is changed; it does not undergo a metamorphosis nor does it ever bear fruit among us, as far as we have noticed hitherto, and it seems to agree with the description of the so-called *Pinus Mugo*, made in Italy by the botanists. If this is not the product of some intermarriage between the Pine and the Fir, we are mistaken on all counts.

The *Lychnis apetala* is constant in the Lapponican Alps, although it grows among the *Lychnis dioica*. Even when this is planted in gardens it is just as constant as in the Alps; we observe with ease

[19] See note p. 171.

that this plant today is distinct; however, it seems quite indubitable to me that it arose first from the *Lychnis dioica*, and especially because of a specimen gathered in Siberia by Dr. Gmelin, such as we do not possess within our own boundaries.

J. C. and J. B.

In October 1754, Dr. Charles Alston, Professor of Botany at the University of Edinburgh, published in the *Gentleman's Magazine* a paper entitled "On the Sexes of Plants."

In this article he attacked the theory of sex in plants and cited a number of instances of pistillate flowers bearing viable seed in the absence of all pollen. As apogamy was unknown at the time, Alston's results seemed to be inconsistent with the assumption that the flowering plants reproduced sexually. In itself, the paper of Alston's is of no great importance, but it drew replies from "two celebrated botanists of North America, both dated June 10, 1755." These letters were published in the September issue of the magazine. Both replies attempted to show that sex must exist in plants by citing instances of known plant hybridization. The letters, to be sure, do not add much to the general knowledge of plant hybrids, but they do show that the scientists in the far-off Colonies kept in touch with developments in the home land. The first letter was signed by the initials "J. C." A celebrated American botanist of this period was John Clayton (1685-1773), who collected the plants for Gronovius' *Flora Virginica*. An interesting feature of this letter is the use of the term "bastard plant" to designate a hybrid. This is one of the earliest examples of such a use of the term. Apparently actual specimens of hybrid plants were sent to the editor along with the letter. From the *Gentleman's Magazine*, 25:407-408 (1755):

Some remarks made on Dr. Alston's Dissertation on the Sexes of Plants, (*see Vol. XXIV, p. 465*) *by two celebrated botanists* of North America, *both dated* June 10, 1755.

Letter I

I was surprised to see in the *Gent. Mag.*, for *Oct.* last, a little essay by Dr. *Alston*, botanic professor at *Edinb.*, endeavoring to overthrow the long established doctrine of the different sexes in plants, and of the necessity of the embrio's being impregnated in some manner by the dust, or farina of the antherae, in order to the seeds being perfect, and prolific, capable of producing a plant again of the same species.

I wonder that some of your botanists in *England*, or other parts of Europe, have not yet answered it, for I have not yet heard that they have.

My opinion on the other side of the question is too well grounded and confirmed, by considering what has been wrote by *Grew*, *Bradley*, *Logan*, *Linnæus*, *Dr. Parsons*, and some others, to be even staggered by those few experiments, which may possibly be accounted for, as the axiom of the generation of plants (being analogous to that of animals) stands still unimpeached.

As first, some species of violets are known to be what *Linnæus* calls *monœcia*, or to have male and female fruitful flowers in the same plant.

Then as to the experiments on the spinach, hemp, mercury, who will venture to affirm, that the farina of flowers cannot be carried a great distance by the wind, and when it comess near enough to the stigmas, be strongly attracted by them, and brought into contact, I know that our female fruit-bearing mulberry and persimmons, frequently grow above a mile distant from the male; and I have two female rhammas's in my garden, which blossom every year, but as there are none of the male species of that shrub in the country, at least near where I live, my female shrubs never yet have perfected their berries.

Then as to the specimens I sent you of the bastard quarnoclif,[20] and other bastard or mule plants, is there not all the reason in the world from thence, and a multitude of other irregular vegetable

[20] Quamoclit, now *Ipomœa Quamoclit*, the Cypress Vine, a relative of the Morning Glory.

impregnations, well known to all botanists, and some gardeners, to conclude, that the same law is established in the main, tho' with some little variety of circumstances, by the great author of Nature, for the continuence of the species of plants, as for that of animals.

J. C.

The second letter is signed "J. B." The obvious inference is that the "celebrated botanist" of these initials was John Bartram, although it is barely possible that the letter might have been written by either John Bard (1716-1799), the well-known anatomist, or by the physician, Josiah Bartlett (1729-1795). If it was written by Bartram, it must have been altered by the editor, for the spelling and the punctuation are but faintly reminiscent of Bartram's other letters. There is also an indication that the editor left out some of the hybridization experiments cited by the writer. In the next to the last paragraph a single instance is cited followed by a blank. The next words are "These experiments." From Vol. 25, p. 408:

Letter II

In the Magazine I read Dr. *Alston's* observations on the mercury, spinage and hemp, the female producing good seed at great distance from the male, which seems curious, and may be true to appearance; yet I can't believe but that the female must be influenced by the male, tho' at a very great distance, as providence acts uniformly in all its operations: But yet it is not impossible, in the case of accidents, but that some provision may be made in the female to act in both capacities, especially in what we call annual plants; that if the female grow at too great a distance from the male to attract his farina, there may be produc'd some latent farina to impregnate the female part, altho' before invisible and unactive, and would have remain'd so, unless called and rouzed up to assist in the greatest end of nature.

Many genusses of plants are male and female in distinct trees, of which I have observed many of the fem. trees to have the same anthera, but not to discharge the farina, unless at a great distance

from the male tree; but this is not always the case; for the roots of *English* briony that I raised bore abundance of fine red berries, but all imperfect, being nothing but skin, and watry juice.

I found a fine stalk of *Indian* corn, at a great distance; I cut off the male tossil as soon as it appeared, and there was produced a large ear, but no good grains upon it.

If we plant cucumbers, squashes, or melons, near the bitter gourd, the fruits of the first will be as bitter as gall. . . . These experiments show how necessary the male farina is to the fructification of all seeds, and how liable plants are to be bastardized by bad neighbors of their own kindred.

This will give a hint, how careful a curious gardener ought to be. The way to preserve a good species of any plant is to keep it separate from others of the same kind, that is not of so good a quality.

J. B.

Christian Ludwig Ramstrom

Christian Ramstrom's paper entitled *Generatio Ambigena* bears the date of December 12, 1759. It was published in Vol. VI of *Amoen. Acad.* The author was not interested in plant hybridization as a phenomenon in itself, but only for its bearing upon the general theories of animal and plant reproduction. After a short discussion of equivocal and univocal generation, he discusses some of the contemporary views of morphogenesis. The hybrids he so inaccurately describes are included to bolster an entirely erroneous theory of sexual reproduction. Ramstrom's careful distinction between the contributions of the father and the mother plant to the hybrid offspring show to what length facts can be selected to prove a thesis. On the other hand, he undoubtedly described some real hybrids.

As far as plants are concerned, we have a shining example here at Upsala in the daughter of the *Veronica Maritima* fertilized by the *Verbena officinalis;* for thus far we observe that the fructification from the medullary substance in this hybrid product is plainly like the mother, while the externals, such as the leaves and the other

corticalia are very like those of the father. It happened several years ago that in a certain packet of the Academic Garden where a *Tragopogon pratense* and the *Tragopogon porrifolium* were growing side by side a plant sprang up which resembled the *Tragopogon pratense*, but with red flowers. Therefore in the year 1757 our President undertook an experiment with regard to a *Tragopogon pratense* which had recently shed its flowers; he blew on them vigorously, shook off the pollen, cut off the flower of the *Tragopogon porrifolium* and lightly sprinkled the pollen genitalia over it; he repeated it for some days in the same flower. This flower eventually passed to the seed stage; the seeds were sown in the year 1758, and flowered in the current year 1759, and bore fruit. It is worth while to note that its flowers or the corollæ showed a purple color almost to the base; that the calyx was longer than in the *Pratense;* and they were somewhat larger than in the usual pedunculum; in a few of them the external parts were like the father, the internal parts like the mother. Perchance the day may come which will show that very many of the *Gerania Africana* and *Mesembryanthemata* and many species of the same genera are perhaps the product of that very circumstance, i.e., that a vagabond father (i.e., pollen carried by the air) has fertilized the mother plant. And although hybrids are often sterile, both in the animal and vegetable kingdoms, this is not, however, universally the case; but admits of many exceptions, at least in the *Tragapogon* named above. Hence on occasion botanists may have new rules, i.e., that as many species may be held to be congenerous as to have been produced from the same medullary substance of the mother. We are taught by the insects not to disturb this arrangement of Nature, for they eat up plants of the same genus which they have not seen before and which were but recently imported from India. But to confirm this thesis I ought in particular to employ reasons taken from the Animal Kingdom. For the laws of generation are the most readily stabilized by adducing the example of animals, where hybrids offer the most apparent guide of all. . . .

In mixtures of this sort of the different species, it must also be observed that occasionally after many generations, the qualities acquired through the father fade out more and more, and the maternal potency, which with the help of the nervous system gradually modifies

the rest of the body to its own peculiar character, finally predominates over the paternal. To me these examples, both in plants and animals, seem so exceedingly clear that if they should prove deceptive, then nothing would be alien to fraud. Hence, I persuade biologists that they should not cease from trying out that pathway with care, and from finding out what the mother contributes to the medullary substance and what the father contributes to the cortical substance, for I do not doubt but that a greater light will shortly arise in these matters. In the meantime I act the part of him who sharpens the sword, though I myself have no part in the cutting. . . .

It is clear from the aforesaid hybrid species that the cortical substance must take substance from the male, for they show that the externals always are assimilated to the father, the internal organs to the mother, both in plants and animals. For if the engendering has no function except to vivify the germ of the mother, the offspring would be entirely similar, no matter what father engendered them, but, as we have said, the external parts are like those of the father.

John Christian Daniel Schreber

Schreber's article, *Theses Medicae*, is dated June 14, 1760. It is by no means a major contribution, and occupies only three pages in Volume VI of the *Amoen. Acad.* It is not an addition to the knowledge of plant hybridization but serves as a sample of the current belief in the existence of plant hybrids. From Thesis number six:

Since, accordingly, it is established from recent observations that hybrid plants are produced and that they are very different in the external appearance as long as their mother has been fertilized by a male of a different species, it seems probable that plants which are similar in their fructification, though different in external structure, have descended from one and the same plant; but whether these are to be called the daughters of time, or whether they were mixed by their Creator in the beginning, a later day will show. Meanwhile, botanists have called these plants which are similar in their fructification, species of the same genus.

From Thesis number ten:

It seems to us evident from the various plants with curly leaves that the odor in hybrid plants is changed fairly often, and makes its appearance as a scent different from that of the mother.

Carolus Linnæus

Contributions by six of Linnæus' students have been recorded in the preceding pages. How much of this work is due to the several students and how much to Linnæus himself is a matter of conjecture. Linnæus certainly followed the investigations of his students very closely and perhaps even directed them step by step, at least he was intimately associated with those students who went beyond mere philosophical speculation. He himself did not publish a comprehensive exposition of plant hybridization until 1760.[21] In that year he entered a contest staged by the Academy of Sciences at St. Petersburg, by submitting an essay entitled *Disquisitio de Sexu Plantarum.* This essay, which was awarded the prize, was published in the *Amoen. Acad.*, Volume X.

In this paper Linnæus was concerned with the proof of the sexual nature of reproduction in the flowering plants, and his description of hybridization was only incidental; but his treatment of the subject was not the mere scholastic discussion that Sachs implied but a very clear and logical presentation of experimental data. The first experiment is described thus:

One evening in the month of August, I removed all the stamina from three flowers of *Mirabilis Longiflora,* at the same time destroying all the rest of the flowers which were expanded; I sprinkled these three flowers with the pollen of *Mirabilis Jalappa;* the seed-buds swelled, but did not ripen. Another evening I performed a similar

[21] He referred to hybrid plants much earlier. In *Hortus Upsaliensis,* Stockholm, 1748, on page 167, occurs: "6. Dracocephalum foliis verticillatis. Haec forte hybrida ex *Nepeta* 3 cuius corrolam & Dracocephalo cuius calykem habet. 7. Dracocephalum floribus verticillatis. Anne heic species novae e diversa copula hybridae?

experiment, only sprinkling the flowers with the pollen of the same species; all these flowers produced ripe seeds.

The essay ends in a relatively lengthy description of hybridization, for Linnæus looked upon the production of hybrids as the final proof of the existence of sex in plants.

Leaving these instances, and innumerable others, which are so well known to botanists that they would by no means bear the appearance of novelty, and can only be doubted by those persons who neither have observed nature, nor will they take the trouble to study her, I pass to a fresh subject, concerning which much new light is wanted; I mean hybrid, or mule vegetables, the existence and origin of which we shall now consider.

I shall enumerate three or four real plants, to whose origin I have been eyewitness.

1. *Veronica spuria*, described in *Amoenitates Acad.* Vol. III, p. 35, came from the impregnation of *Veronica maritima* by *Verbena officinalis;* it is easily propagated by cuttings, and agrees perfectly with its mother in fructification, and with its father in leaves.

2. *Delphinium hybridum*, sprung up in a part of the garden where *Delphinium clatum* and *Aconitum Napellus* grew together; it resembles its mother as much in its internal parts, that is, in fructification, as it does its father (the *Aconitum*) in outward structure or leaves; and, owing its origin to plants so nearly allied to each other, it propagates itself by seed; some of which I now send with this Dissertation.

3. *Hieracium Taraxici*, gathered in 1753 upon our mountains by Dr. Solander, in its thick, brown, woolly calyx, in its stem being hairy towards the top, and in its bracteæ, as well as in every part of its fructification, resembles so perfectly its mother, *Hieracium alpinum*, that an inexperienced person might mistake one for the other; but in the smoothness of its leaves, in their indentations and whole structure, it so manifestly agrees with its father, *Leontodon Taraxacum* (Dandelion), that there can be no doubt of its origin.

4. *Tragopogon hybridum* attracted my notice the autumn before last, in a part of the garden where I had planted *Tragopogon pratense*, and *Tragopogon porrifolium;* but winter coming on, destroyed

CAROLUS LINNÆUS

its seeds. Last year, while the *Tragopogon pratense* was in flower, I rubbed off its pollen early in the morning, and about eight o'clock sprinkled its stigmata with some pollen of the *Tragopogon porrifolium*, marking the calyces by tying a thread round them. I afterwards gathered the seeds when ripened, and sowed them that autumn in another place; they grew, and produced this year, 1759, purple flowers yellow at the base, seeds of which I now send. I doubt whether any experiment demonstrates the generation of plants more certainly than this.

There can be no doubt that these are all new species produced by hybrid generation. And hence we learn, that a mule offspring is the exact image of its mother in its medullary substance, internal nature, or fructification, but resembles its father in leaves. This is a foundation on which naturalists may build much. For it seems probable that many plants, which now appear different of the same *genus*, may in the beginning have been one plant, having arisen merely from hybrid generation. Many of those Geraniums which grow at the Cape of Good Hope, and have never been found wild anywhere but in the south parts of Africa, and which, as they are distinguished from all other Geraniums by their single-leaved calyx, many-flowered foot-stalk, irregular corolla, seven fertile stamina, and three mutilated ones, and by their naked seeds furnished with downy awns; so they agree together in all these characters, although various in their roots, stems, and leaves; these Geraniums, I say, would almost induce a botanist to believe that the species of one *genus* in vegetables are only so many different plants as there have been different associations with the flowers of one species, and consequently a *genus* is nothing else than a number of plants sprung from the same mother by different fathers. But whether all these species by the offspring of time; whether, in the beginning of all things, the Creator limited the number of future specimens, I dare not presume to determine. I am, however, convinced this mode of multiplying plants does not interfere with the system or general scheme of nature; as I daily observe that insects, which live upon one species of a particular *genus*, are contented with another of the same *genus*.

A person who has once seen the *Achyranthes aspera*, and remarked its spike, the parts of its flowers, its small and peculiarly formed nec-

taria, as well as its calyces bent backwards as the fruit ripens, would think it very easy at any time to distinguish these flowers from all others in the universe; but when he finds the flowers of *Achyranthus indica* agreeing with them even in their minutest parts, and at the same time observes the large, thick, obtuse undulated leaves of the last-mentioned plant, he will think he sees *Achyranthus aspera* masked in the foliage of *Xanthium strumarium*. But I forbear to mention any more instances.

Here is a new employment for botanists, to attempt the production of new species of vegetables by scattering the pollen of various plants over various widowed females. And if these remarks should meet with a favorable reception, I shall be the more induced to dedicate what remains of my life to such experiments, which recommend themselves by being at the same time agreeable and useful. I am persuaded by many considerations that those most numerous and most valuable varieties of plants which are used for culinary purposes, have been produced in this manner, as the several kinds of cabbages, lettuces, etc.; and I apprehend this is the reason of their not being changed by a difference of soil. Hence I cannot give my assent to the opinion of those who imagine all varieties to have been occasioned by change of soil; for, if this were the case, the plants would return to their original form, if removed again to their original situation.

V

RÉSUMÉ OF LATER HYBRIDIZATION

I. KNOWLEDGE OF PLANT HYBRIDIZATION AT THE TIME OF KOELREUTER

THE *Disquisitio de Sexu Plantarum* of Linnæus was the last contribution to plant hybridization which appeared before the epoch-making work of Koelreuter. It is true that a pupil of Linnæus', Johannes Mart. Gråberg, cited some instances of plant hybridizing in his dissertation, *Fundamentum fructificationis* (Oct. 16, 1762), but this work appeared after Koelreuter had published his first paper on the subject, Part I of the well-known *Vorlaufige Nachricht von Einiger das Geschlecht der Pflanzen*, Leipzig, 1761. In spite of this, Gråberg really belongs with the plant hybridizers who preceded Koelreuter, for the general tone of his paper is like that of the other essays of the period, and his scientific standards do not differ from those of the other members of the Linnæan school. His paper has been summarized very adequately by Roberts (1929), however, and there is no need of its being quoted here.

The publication of Koelreuter's experiments marks the beginning of a new period in the history of genetics. His scientific outlook was remarkably modern and his papers read as if they had been written in the twentieth century. His investigations were carefully designed and systematically carried out, and, although many nineteenth-century botanists succeeded in overlooking his work, he furnished a durable scientific basis for genetical experimentation. His contributions will not be described here, for his papers have been reprinted and are available in Ostwald's *Klassiker der exakten Wissenschaften* (Number 41). In addition, an excellent résumé in English has been published by Roberts (1929).

Koelreuter's scientific achievements were not immediately appreciated. In fact, it was nearly a hundred years later, in the time of Darwin, Nägeli, and Mendel, that he first received the recognition which was his due. Since then the value of his work has been acknowledged, although it has remained the fashion to underestimate the work of all plant hybridizers who preceded him. It is true that the earlier investigators did not take themselves with the seriousness which we associate with sound scientific research, nor did they record their findings in the form to which we have become accustomed. Most of their observations were casual, many were reported simply as natural curiosities, but a few, obtained from well-designed experiments, were presented carefully and accurately. These latter deserve more attention than they have received. The ignoring of their existence prevents an accurate evaluation of Koelreuter's work and assigns him a priority he neither needs nor deserves. This is regrettable, for any history of a science which overlooks whole masses of minor contributions gives an erroneous picture of development, for it presents only a few outstanding discoveries against a distorted background.

The knowledge of animal and plant hybrids increased extremely slowly. Even before the advent of civilization, spontaneous hybridization must have been frequent in the various cultivated crops and in the different breeds of domestic animals. These hybrids were not recognized, for they could not be distinguished easily from true species. For nearly 2,500 years their existence was not suspected, for the only known mark of a hybrid was sterility, and the offspring of these species crosses were often fertile. It was not until sex in plants was discovered that any real progress was made. Then the simple technique of cross pollination made an entire realm available for experimentation.

It is interesting to note that the investigations of plant hybridization were not stimulated by the evidences of hybrid-

ity in the plants themselves, but by the concatenation of two bits of knowledge; first, that animal hybrids could be obtained through a sexual union of unlike forms and, second, that plants reproduced sexually. At first the plant hybrids were sought not so much for themselves as for the proof they gave of the fact that sexual reproduction occurred in the vegetable kingdom. Later, the possibility of the production of new and valuable forms was recognized and the practical value of hybrids understood.

The direct modification of the endosperm by pollen, known as "xenia," played an important rôle in the discovery of plant hybrids. Indeed, the effects of foreign pollen were noted long before the causal agency was suspected. From Tabernaemontanus (1588) to Monti (1719) some twenty-two individuals recorded the occurrence of several types of grain upon a single ear of corn, although they did not know what caused the mixture. This spectacular example of xenia finally led to the correct interpretation of the mixing of varieties and to the first recorded instance of plant hybridization. The spontaneous crossing of varieties in *Zea Mays* was described by Cotton Mather, Paul Dudley, Benjamin Cooke, Pehr Kalm, and William Douglass.

Some of the effects of hybridization described by the early investigators may be the result of metaxenia. This interpretation will have to be received with caution, for the records can hardly be taken at their face value. Cotton Mather and J. B. (John Bartram?) stated that foreign pollen altered the taste of cucumbers and melons. Metaxenia in apples was described by Bradley and Cooke, but as they were not able to allow for possible bud-sports, their records are not altogether convincing. But aside from all such evidences of hybridity, furnished by xenia and metaxenia, proof of the crossing of different types was supplied by the production of numerous hybrid or mule plants. These were found in many different

genera and were recorded by numerous botanists. A hybrid *Dianthus* was described by Fairchild and Knowlton, and hybrid *Auriculas* by Bradley, Rudberg, and Guyot. Hybrids were also noted in *Mercurialis* (Marchant, Rudberg, Haartman), in *Brassica* (Miller, Wahlbom, Haartman, Mylius), in *Lychnis* (Bartram), in *Peloria* (Rudberg), in *Saxifraga* (Rudberg, Haartman), in *Delphinium* (Rudberg, Gmelin, Linnæus), in *Tulipa* (Wahlbom, Guyot), *Veronica* (Haartman, Ramstrom, Linnæus, in *Ipomœa* (J. C.), in *Tragopogon* (Haartman, Ramstrom, Linnæus), and in *Mirabilis* and *Hieracum* (Haartman, Linnæus). Thus, by 1761, when Koelreuter published his first paper, many instances of plant hybridization were already known, and hybridity was well understood.

2. SUBSEQUENT DEVELOPMENT OF GENETICS

After the publication of Koelreuter's work there was a marked hiatus in the investigation of hybrid plants, and it was not until nearly the end of the century that Sprengel (1793) and Knight (1799) published their investigations. Then there was another gap—this time of twenty years—before the works of Herbert (1819) appeared. He was followed by Goss (1820), Seton (1824), Sageret (1826), Gärtner (1827), Weigmann (1828), and Henslow (1833). Only four more hybridizers of note had published by the middle of the nineteenth century; André Vilmorin (1840), Gordron (1844), Lecoq (1845), and Regel (1848). Naudin published in 1855, and Louis de Vilmorin and Charles Darwin in 1859. During the next decade, just a hundred years after Koelreuter, there was a real revival of interest in hybridization, and in a short period the contributions of Henry de Vilmorin (1863), Duchartre (1863), Mendel (1865), Nägeli (1865), Wichura (1865), Verlot (1865), Laxton (1866), and Hoffman (1869) were issued. Although the

significance of Mendel's discoveries was not understood, and his results were buried for thirty years, the rapidly increasing interest in hybridization, and the numerous experimental attacks on the problem, made the rediscovery of his laws certain.

It is not necessary to mention here the many noteworthy contributions to the knowledge of hybrids which appeared between Koelreuter and the rediscovery of Mendel. Roberts has covered this ground very adequately. Two papers, however, deserve particular attention, as both authors independently noted some of the peculiarities of Mendelian inheritance. G. W. McCluer in an article entitled *Corn Crossing*, published in 1892, called attention to the heterogenous condition of the first generation hybrids, and to the reappearance of the parental types in subsequent generations. He also recognized clearly the value of the F_2 generation in genetical investigations. W. J. Spillman published *Quantitative studies on the transmission of parental characters of hybrid offspring* in 1901, before he had seen Mendel's paper, which had just been brought to light. From experiments in wheat crosses, started in 1899, he found that the first generation had almost no variations, but that the second hybrid generation split up into many different types, incidentally with the recombination of many of the parental characteristics. He noted also the relative numbers of the different types.

By 1900 so many careful investigations of hybridity were under way that it is not surprising that Mendelian inheritance and Mendel's own publication were discovered. Three investigators working independently found Mendel's paper—De Vries, Correns, and Von Tschermak—and with the rediscovery of Mendel, modern genetics was born.

APPENDIX

A CHRONOLOGICAL LIST OF HYBRIDIZATION, 1716-1760

1716—Cotton Mather described the crossing of different color varieties of Indian Corn (*Zea Mays*) in a letter to James Petiver, dated September 24, 1716. He also reported the pollination of squash (*Cucurbita Pepo* var. *ovifera*) by gourds (*C. Pepo* var. *condensa* or *C. maxima*). These crosses were later included in his book, *Religio Philosophica* or *The Christian Philosopher*, London, 1721.

1717—Thomas Fairchild fertilized the carnation, *Dianthus caryophyllus*, with the pollen from the Sweet William (*D. barbatus*). This is the first recorded artificial hybrid.

1717—Richard Bradley noted spontaneous hybridization in *Auricula* (*Primula & Auricula*). He also noted the effects of foreign pollen upon the appearance and flavor of apples (*Pyrus Malus*) (metaxenia?). He warned against the contamination of melons (*Cucumis Melo*) by the pollen of cucumbers (*Cucumis sativus*), and stated that he was attempting to hybridize wall flowers (*Matthiola*).

1719—Jean Marchant reported the sudden appearance of a new form of *Mercurialis* to L'Academie Royal des Sciences de Paris. The production of this new variety was probably due to Mendelian segregation. The segregants (two plants) were both male. As the new type continued to reappear in subsequent years, there must have been either a back-crossing of the segregant to the parental type, or else the latter, being heterogeneous, continued to segregate.

1720—William Knowlton found and described a spontaneous hybrid in the genus *Dianthus*. The existence of this hybrid was made known to the Royal Society by Patrick Blair.

1721—Philip Miller described a number of variety crosses within the genus *Brassica* to Patrick Blair, in a letter written on October 19, 1721. He also recorded these hybridizations in the *Gardeners' Dictionary*, 1724, 1731, etc.

1724—Paul Dudley described wind pollination and variety crosses in *Zea Mays* in a paper in the *Philosophical Transactions*, 33:194-200.

1728—Henri Louis du Hamel discussed the bearing of plant hybridization upon the formation of new varieties and species in *Recherches sur les causes de la multiplication des especes de fruits.*

1729—Thomas Henchman observed variety crosses in *Pisum* and noted the occurrence of different-colored peas in the same pod. These he described in a letter to Sir Joseph Ayloffe, dated June 3, 1731. On July 1 of that year Sir Joseph read the letter to the Royal Society.

1734—Jacob. Andr. Trembley in *Theses Physical de Vegetatione et Generatione Plantarum* discussed the formation of plant hybrids.

1738—John Mitchell wrote *Dissertatio brevis de principiis botanicorum et zoologicorum* in 1738 and published it in the *Ephemerides Leopoldina* in 1748. This was later reprinted as a separate in 1769. In this article Mitchell discussed plant hybridization and attempted to place taxonomy on a genetic basis.

1739—John Bartram stated in a letter to Col. Wm. Byrd that he had crossed different species, obtained strange hybrids, and hoped to develop new horticultural varieties. There is evidence that he also described these results to Peter Collinson and to Gronovius. A manuscript in Bartram's handwriting describes hybridization in *Lychnis.*

1744—Daniel Rudberg in his dissertation on *Peloria* described the plant as a hybrid descended from *Linaria* and another unknown parent. He included in his article a discussion of plant hybridization in general.

1745—Johann Georg Gmelin, in a letter dated May 17, 1745, reported the appearance of new forms of *Delphinium* which he assumed to be hybrids. He later published a description of these forms in *Flora Siberica*, St. Petersburg, 1749. His longest and most complete discussion of plant hybridization was

Sermo academicus de novorum vegetabilium post creationes divinam exortu, Tubingae, 1749.

1745—Benjamin Cooke described the effect of foreign pollen upon several varieties of apples (*Pyrus Malus*) in letters to Peter Collinson, dated October, 1745, December 4, 1748, and one some time in 1749. In the latter communication Cooke described the crossing of different color varieties in *Zea Mays*.

1746—Johannes Wahlbom described hybridization in *Tulipa* in *Sponsalia Plantarum*, Stockholm, 1746. He also explained the "degeneration" of *Brassica*, which had previously been recorded by Morison (1680) and Ray (1686), as the result of a contamination by the pollen of wild varieties.

1750—Pehr Kalm described variety crosses in *Zea Mays* in a paper *Beskrifing om Mays* published in Vols. 12 and 13 of the *Kongl. Svenska. Vetensk. Acad. Handlingar*.

1751—William Douglass described the mixing of color varieties in *Zea Mays* in *A Summary Historical and Political of the First Planting etc.*, Boston, 1749-51.

1751—Johannes Haartman in *Plantae Hybridae* (November 23, 1751) assumed on taxonomic grounds that a number of varieties are hybrids. He mentioned, among others, *Veronica*, *Delphinium*, *Saponaria*, *Acteae*, etc.

1751—Christlab Mylius in *Physikalichen Belustigungen* (Vol. I, p. 81-96) described variety crosses in *Brassica*.

1752—Edmé Gilles Guyot published directions for crossing the different color varieties of a species and described his own crosses in *Auricula* (*Primula Auricula*). This essay, *Sur les fleurs et sur les causes de la variété de les couleurs* was published in *Observations sur l'histoire naturelle la physique et la peinture* (Vol. I, pt. 1, p. 75).

1752—James Parsons in *Philosophical Observations on the Analogy between the Propagation of Animals and that of Vegetables* described plant hybrids but explained their sterility on theological grounds.

1752—Johannes Gessner in *Dissertatio physica de Ranunculo bellidiflora et plantis degeneribus*, Tiguri, 1753, discusses hybridization and the production of new varieties.

1755—Nicol Dahlberg described a number of animal hybrids in *Metamorphosis Plantarum* (June 3, 1755), and interpreted certain plants, which were difficult to classify, as hybrids.

1755—In the *Gentleman's Magazine* of September 1755, there were published two letters from "two celebrated botanists of North America." The first, signed J. C. (John Clayton?) described hybridization in *Ipomœa;* the second, signed J. B. (John Bartram?) also discussed plant hybrids and described cross pollination in *Cucumis.*

1759—Christian Ramstrom in *Generatio Ambigena* (December 12, 1759) discussed the relative importance of the male and the female parent in plant hybridization.

1760—Johan Schreber (*Theses Medicae,* June 14, 1760) held it probable that related varieties may be descended from the same maternal parent crossed with different males.

1760—Carolus Linnæus, in *Disquisitio de Sexu Plantarum* describes the experiments which produced hybrids in *Mirabilis, Veronica, Delphinium, Hieracium* and *Tragopogon.*

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